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RESULTS OF THE ARCHBOLD EXPEDITIONS PAPUAN NOTHOFAGUS

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With twenty-two figures and frontispiece

CONTENTS

	PAGE
Introduction	301
Plant geographical significance	302
Ecological remarks	313
Parasites of Nothofagus	317
Evaluation and variation of characters	318
Generic differences between Fagus and Nothofagus	326
Subdivision of Nothofagus with a key to the species	328
Specific distinction in Papua	339
Keys to and descriptions of the Papuan species	341
Bibliographic references	372
Index to fagaceous names	374

ONE OF THE MOST REMARKABLE FINDS of the Third Archbold New Guinean Expedition has been the discovery of extensive forests in New Guinea in which the fagaceous element dominates the framework of the canopy. Representatives of *Nothofagus* are very common among these fagaceous dominants.

The big size of the trees is probably one of the reasons why this genus has been overlooked in the often hurried field work during the expeditions to the interior of the island. However, field workers with more leisure, as, for example, Lauterbach, Ledermann, Miss Gibbs, and even Lane-Poole,

apparently failed to collect *Nothofagus*, unless their material was not recognized and remains concealed among *incertae sedis* of some other family.¹

There is another reason for this neglect in collecting *Nothofagus*, and that is that the ♀ flowering is very inconspicuous, and that the more showy and abundant ♂ flowers are only present during a remarkably short "flush" period, as in *Fagus*. Besides the arboreal habit the flowering itself makes *Nothofagus* unattractive to the field botanist.

From these considerations it is quite understandable that the first collection, as far as known, was by Dr. A. A. Pulle (nestor of Dutch systematists and my revered teacher) under favourable circumstances, from a stunted shrub in anthesis on the crest of Mt. Hellwig, in 1913. Over twenty years elapsed before the genus was collected again, this time by C. E. Carr in 1935–1936. After that collections came in independently very rapidly, by Clemens in 1937, Brass and Brass & Versteegh in 1938–1939, Kanehira & Hatusima in 1940, and Eyma in the same year. After the war several more new collections were made by A. J. G. H. Kostermans on Mt. Arfak and by the collectors of the N. G. F. series, L. S. Smith, J. S. Womersley, J. Cavanaugh, and A. J. Schindler.

The assemblage of these collections, totaling forty-seven, which has been generously put at my disposal during several years, forms the basis of this paper. It shows that the genus is distributed through the mountains of the island, between 1000 and 3000 m. altitude.

I have to express my gratitude for loan of collections to the Keeper of the Herbarium Bogoriense, the Director of the Arnold Arboretum, the Forest Botanist at Lae, the Director of the Fielding Herbarium of Oxford University, and the Director of the Herbarium of Utrecht University. In addition I have the privilege of rendering special thanks to the following individual botanists who assisted me in various ways: Dr. R. C. Bakhuizen van den Brink, Jr., Leyden, Dr. M. G. Baumann-Bodenheim, Zürich, Dr. B. K. Boom, Wageningen, Mr. L. J. Brass, Florida, Mr. A. A. Bullock, Kew, Miss Isabel Cookson, Melbourne, Dr. H. E. Dadswell, Melbourne, Dr. W. M. Docters van Leeuwen, Leersum, Netherlands, Mr. L. L. Forman, Kew, Dr. E. Kausel, Santiago de Chile, Mr. P. W. Leenhouts, Leyden, Dr. E. D. Merrill, Jamaica Plain, Mass., Miss L. M. Perry, Jamaica Plain, Mass., Dr. C. Skottsberg, Stockholm, Dr. H. Sleumer, Leiden, Dr. W. T. Stearn, London, the late Mr. C. T. White, Brisbane, and Mr. J. S. Womersley, Lae.

PLANT GEOGRAPHICAL SIGNIFICANCE

As to the geographical range, there is nothing unique about the occurrence of *Nothofagus* in New Guinea. Its generic area fits in satisfactorily with that outstanding set of microtherm, now subantarctically distributed

¹ Sterile sheets can immediately be recognized by the remarkable (sometimes early caducous) peltate stipules, the distichous leaves with a sulcate midrib and a glandular undersurface, and the resinous collectors on the adaxial base of stipules and perular bracts.

genera ranging from Chile to Fuegia, the Subantarctic Islands and New Zealand to the Tasmanian and Victorian Alps, often extending their area to New Caledonia¹ — sometimes also including Queensland — and protruding into Malaysia,² primarily into the Alps of New Guinea, often prolongating their track to the high peaks of Ceram, Central Celebes, the Philippine Islands, Mt. Kinabalu, and in single cases even to the Malay Peninsula and N. Sumatra (*Oreobolus*), as revealed by my exploration of the Gajo Lands in North Sumatra (3).

Prof. Diels, in his contribution to an analysis of the Papuan mountain flora (1), had already grasped this generality, and as early as 1930 had included *Nothofagus* in his list of subantarctic elements as a genus which would likely turn up at least in the Island of New Guinea. Since he made this list, this and other remarkable additions have indeed been recorded, mostly from the Archbold-Brass collections, supplementary to those which I had listed in 1934 (2). There is little doubt that several others will be collected later or have already been collected and are waiting identification.

This group includes *Plantago* § *Plantaginella*, *Araucaria*, *Scleranthus* § *Mniarum*, *Libertia*, *Carpha*, *Pratia*, *Oreomyrrhis*, *Coriaria* § *C*, *Eulibocedrus*, *Drapetes* (incl. *Kelleria*), *Erechtites*, *Abrotanella*, *Oxalis magellanica*.

Some of these, like *Pratia*, have reached the southeastern part of the Asiatic continent, and a typical one, *Euphrasia*, of which the greatest morphological polymorphy is found in Subantarctica, is spread over the Northern hemisphere. In contradiction to Du Rietz and others, *Euphrasia* seems to me to represent a subantarctic element on the Northern hemisphere, and not the reverse.

The set of areas just mentioned, manifestly bound to a wet and cool to cold climate, is one of a group of four types of southern distribution which appear to make part of the development or represent relics of the former spread of ancient distribution on the Southern hemisphere. The set just mentioned, which I call *type I*, is restricted to *circum-South Pacific distribution*.

A second set of areas of smaller size (*type II*) could be called *Australasian areas*, comprising Australia, Tasmania, New Zealand, and extending towards Eastern Malaysia. To this set belong *Myriophyllum* § *Pelonastes*, *Bubbia*, *Diuris*, *Pterostylis*, *Thelymitra*, *Olearia*, *Quintinia*, *Phyllocladus*, *Trachymene*, *Corybas*, *Patersonia* (absent from New Zealand), *Diche-lachne*, *Cotula* § *Leptinella*, and *Centrolepis*.

There is a great affinity between these two types, which form only variations on one basic pattern. For instance, *Centrolepis* belongs to type II, but the Centrolepidaceae as a whole to type I, *Kelleria* to type II, but *Drapetes* s.l. to type I.

A third set of areas of larger size which belongs to the same pattern occupies the area of type I, but in addition also extends to the East to

¹ And sometimes to other adjacent islands within the andesite line: Fiji, New Hebrides, and Solomons.

² Sometimes without occurring in Australasia, like the *Corsiaceae*.

the Central Pacific Islands (e.g., Hawaii, Juan Fernandez). This type has been termed *old-Oceanic* (*type III*). To this type can be assigned the genera *Oreobolus*, *Uncinia*, *Coprosma*, *Hebe*, *Muehlenbeckia*, and *Lagenophora*.

Type III comprises apparently also several genera endemic in New Guinea, the alliance of which definitely points to the Pacific and which represent ancient relics now confined to small refuges, for instance, *Papuzilla*, *Brachionostylum*.

Also there are intermediates between type III and type II, as *Ascarina*, *Hecatactis*, and *Tetramolopium*.

A fourth type is that which conforms either to type I or type III, but in addition its representatives occur also outside the Pacific circle; they may be found in remote islands in the S. Indian and Atlantic Oceans, in S. Africa, in Madagascar, or in the Mascarenes. I should like to call this *type IV: General Subantarctic*. Examples of this type IV are: *Acaena*, *Astelia*, *Gunnera*, *Nertera*, *Brachycome*.

This type also shows intermediates with others, e.g., with type II, the Australasian one, in *Hibbertia*.

The sequence of gradual extension in size from type II, via I, and III, to IV, the fact that these genera occur in the same or similar associations and under similar climatological conditions, all more or less microtherm in character, and further, the occurrence of typical intermediates between the types, show that they belonged to similar conditions in the past and have made a part of one regime. The big disjunctions, further, indicate that they represent relics of former distributions in the Southern hemisphere. In considering these disjunctions I agree with Diels, Skottsberg, Du Rietz, and many others, that there is no escape from accepting ancient continental land in the Southern hemisphere, bringing together here what is now remote.

To date this southern land, to fit it into geological history, and to delimit precisely its various subsequent borders, are exceptionally difficult, since no definite palaeogeographic sources can guide us. But, judging from what is known of plant distribution just brought to the fore, and what is known with certainty from other sources, these distributions date at least back to Old Tertiary or even Cretaceous time. What we observe of these distributions at present is a mere chance fraction of what has been.

Among the larger continental islands, New Guinea occupies a predominant place as a refuge of these relics.

One wonders why these distributions, accepted as very ancient, are still limited to the Southern hemisphere theatre. Why have they not dispersed themselves more widely and frequently during this enormous lapse of time into the Northern hemisphere, like *Euphrasia*? Why do so few of the wide areas flare out only to the southeastern corner of continental Asia with stray representatives like *Centrolepis*, *Pratia*, *Nertera*, *Corybas*, and others?

There are not, and in all probability there never were climatic obstacles to a further dispersal of *Nothofagus* into Malaysia.

Nothofagus requires a cool, constantly humid climate. These conditions, however, are not peculiar to the island of New Guinea but are common to the vast majority of Malaysian mountains, as well as to large tracts of the Sino-Himalayan ranges.

Species of both deciduous and evergreen sections show a similar response to constantly humid conditions, though the first has a hygromorphic and the latter a distinctly xeromorphic leaf anatomy, both inside and outside the tropics.

Generalizing, several major groups (affinities) of the plant world possess a northern hemisphere complement to one in the southern hemisphere, and, though their areas may overlap, they more or less exclude each other, e.g., Ericaceae and Epacridaceae, *Dillenia* and *Hibbertia*, etc. With the Fagaceae the genera *Fagus*, *Quercus* s.l., and *Castanopsis* together practically exclude the area of *Nothofagus*.

Southern hemisphere *Nothofagus* and Northern hemisphere *Fagus*, mutually more closely allied than to any other genus, represent, as *Fagoideae*, a marked example of bi-polar distribution, a plant-geographical topic of considerable importance, of which Du Rietz (51) has recently given an exhaustive classical survey.

For an explanation of this bi-polar distribution there are two possibilities.

First, the northern and southern hemisphere complements can be assumed to be descendants of an earlier common worldwide (or at least tropical and subtropical) distributed matrix and to have evolved and spread more or less independently, the one towards northern and the other towards southern regions.

Or, secondly, one of the complements may be more ancient than the other and has produced the other complement, but through later isolation the other has diverged *in situ*, while the ancestral matrix of the one became extinct in that hemisphere.

Both possibilities may have come true in different groups, as there are examples for both.

A marked example for the first possibility is the area of *Euphrasia*, which shows a remarkably uninterrupted distribution from the southern to the northern hemisphere. If the area had been very disjunct in the subtropics and tropics and the two populations had differed a little more, systematists could easily have distinguished two different genera.¹

Examples for the second possibility (extinction) are based on palaeontological evidence of *Araucaria* in the northern hemisphere, living *Araucaria* being restricted to the southern hemisphere. A similar example is that of *Libocedrus*, of which the disjunct northern hemisphere areas have been recently found to support a genus distinct from that of the southern hemisphere.

Engler (40) was inclined to accept for *Fagus-Nothofagus* the first explanation, assuming an ancient, extinct, common ancestry in Malaysia.

It is certainly most remarkable that the areas of *Euphrasia*, *Fagus* and

¹ As a matter of fact two separate genera, *Siphonidium* and *Anagosperra*, have been proposed to accommodate the long-tubed New Zealand species.

Nothofagus, *Araucaria* (living and fossil), and *Libocedrus* are obviously essentially conformal and represent "equiformal relic areas." If they were only seemingly so, it would be an extraordinary coincidence that *Nothofagus* forms, in South America, a substage in the *Araucaria* or *Libocedrus* forest, and that the genera just mentioned all grow together in Patagonia and in the Papuan mountains!

Is it not true that some of these southern hemisphere floral elements were in very ancient time very widely distributed in northern regions, as fossil *Araucaria* seems to indicate? Has not this flora been retreating since, giving us the impression that they are truly southern hemisphere genera now engaged in invading the northern hemisphere via the tropical "bridges"?

Could it not be that *Euphrasia* is one of the very few survivors showing this ancient distributional type, as well as the Fagoideae?

Why *Euphrasia* has maintained itself as one genus on both hemispheres, whereas *Fagus* and *Nothofagus* have been segregated from a common ancestor and represent distinct genera, is a question difficult to answer, as it concerns questions of genetic potentialities which are untraceable and will, in all probability, differ from taxon to taxon.

There is, of course, reason to accept neither an exclusive "monoboreal relic hypothesis" as advanced by Thiselton-Dyer (52) nor an equally exclusive "mono-antarctic relic hypothesis" as advocated by Copeland for the Pteridophytes — and in extreme form by Croizat for the Phanerogams in his recent Manual. Both hemispheres had, it stands to reason, their own autonomous Phanerogamic flora from a common more ancient matrix. There has been no monopoly of either of the hemispheres: plants have extended their areas both from the South towards the North and in the reverse direction. How the epiontological taxonomy and geography have evolved for each individual group can only be ascertained by considering the geographic position of its present living relics in the regime of its taxonomic affinities. This is for isolated, ancient groups like *Nothofagus* a most delicate task to perform.

For several of these groups I am inclined to accept the idea of an early general retreat (extinction), cq. isolated instances of evolution in the northern hemisphere of so-called southern hemisphere plants which formerly enjoyed world-wide distribution. Fossil finds in the northern hemisphere whose identification is beyond question might prove this. If it should turn out to be true, many southern hemisphere groups represent living fossils, as has been suggested before (52). A northern hemisphere fossil record from the Eocene of England, *Dicotylophyllum stopesae*, was described in detail by Miss Bandulska (57) and considered to represent a *Nothofagus* on the strength of the structure of leaf cuticles with particular reference to the stomata.

Returning to factual data, Papuan *Nothofagus* gives definite additional support to the relatively great age of these distributions. Darrah (58), reviewing the evidence, states that the family Fagaceae "was spread to all continents including the Antarctic in the upper Cretaceous." This is

supported by Te Punga (59) who recorded a *Nothofagus* pollen form also from New Zealand Cretaceous beds.

Papuan *Nothofagus* is, most probably, a living fossil similar to, though less spectacular than *Metasequoia*. This has been found by Miss Isabel Cookson, who has described its pollen type from fossil Oligocene or Miocene Australian soils. The pollen type she described could not be assigned to any *living Nothofagus* until she got material from some living species of Papua and New Caledonia (5). Miss Cookson is strongly convinced that the fossil record shows that the type of *Nothofagus* now still thriving in and confined to New Guinea and New Caledonia had been growing in Australia in former geological epochs. She has found this fossil pollen type widely distributed in Australia, from southern Queensland to Tasmania and westward into South Australia. According to R. A. Couper (46) similar, if not identical, "intermediate" pollen species have been distinguished in Cretaceous and Tertiary beds in New Zealand. Apparently the Australian climate in the Cretaceous was colder than it is now. The early Tertiary in Australia was characterized by abundant rainfall and moderate temperatures, according to Wood (53), as shown by the fossil distribution of mesic elements of the rain-forest — to which recent *Nothofagus* in Australia is also confined — which was then much more extensive than it is at present. According to Miss Cookson (4, 5) *Nothofagus* is a most conspicuous pollen in the Oligocene and Miocene deposits from South Queensland to southeastern Victoria, eastern South Australia and Tasmania, as well as in New Zealand, being found in lignites, clays, and mudstones in sheets which are sometimes over 300 m. thick. Pollens belong to at least nine species and occur in vast numbers. Besides the two types of living Australasian species, there are seven more fossil pollen types, one of which is represented by the living Papuan species.

Additional support for the high antiquity of Papuan Fagaceae is rendered by the judgment of F. Markgraf, who in 1925 remarked (7) that, though the number of living Fagaceae at that moment known from New Guinea was small, they were remarkable and of importance for phylogeny: of both *Lithocarpus* and *Pasania* markedly primitive forms were found among the assemblage.

As Torres Straits represents an abrupt demarcation of Fagaceous occurrence (*Quercus* s.l. and *Castanopsis*) towards the Pacific and Australasia, it is highly noteworthy to find just near that border such ancient forms. This again points to a prolonged ancient functioning refuge of the New Guinean continental mass and to long periods of relative isolation both from Australia and Melanesia and from the western parts of Malaysia.

Thus New Guinea is in the unique position of sheltering most primitive northern hemisphere Fagaceae together with living fossils of southern hemisphere representatives.

The intimate botanical affinity between the New Guinean and New Caledonian floras, especially with regard to ancient southern hemisphere genera, is strongly supported by the finding in New Caledonia of several species of *Nothofagus* of the Papuan type. Other taxa supporting the

rather close affinity of New Guinea and New Caledonia are *Agathea*, *Antholoma*, *Bubbia*, *Dubouzetia*, *Durandea*, *Joinvillea*, *Meryta*, *Tapeinosperma*, and *Nepenthes vieillardii* Hook. f.

This discovery we owe to Dr. M. G. Baumann-Bodenheim¹ of Zürich, who, enthused by a hint from Prof. Dr. H. J. Lam, has been on the lookout especially for *Nothofagus* during his recent long-range exploration of New Caledonia. During a visit to Zürich in 1952 I presented my data to Prof. Däniker and Dr. Baumann, and the latter courteously showed me his specimens, which belong to five undescribed distinct species. All of them are coarse in foliage and possess cupules like those of *N. grandis*, *N. brassi*, and *N. dura*. No small-leaved representative seems to occur in New Caledonia. Moreover, all New Caledonian species show three nuts per cupule; one-flowered species seems to be absent.

Therefore, although the New Guinean and New Caledonian floras again exhibit their close affinity and show that they have equal standing as the result of a parallel, comparable geological history, New Guinea seems to be the richer as far as *Nothofagus* is concerned. Its morphological diversity is notably greater in New Guinea than in New Caledonia. Reduction phenomena occurring in the cupule of New Guinean species are remarkable, as will be explained below.

Moreover, New Guinea seems to exceed New Caledonia in number of species, and, though the state of the material is not what it should be and the systematic treatment is, in all probability, unfortunately not to be regarded as final, I am convinced that this number will not be reduced below ten distinct species, even when more ample material has come to hand.

This shows that the Papuan-New Caledonian section is by no means a small part of the genus. It is merely by priority of collections and descriptions that *Nothofagus* has been listed, plant geographically, as a "subantarctic" genus, which it still is, but in a much broader sense. It cannot be denied that by the new finds the main point has been appreciably shifted towards the West Pacific.² With sixteen species in New Guinea and five in New Caledonia the Papuan-Melanesian centre stands at least on an equal footing with the South Pacific area of distribution as far as number of species is concerned.

For the appreciation of the New Guinean-New Caledonian *Nothofagus*, which together form a special taxon, sect. *Planae* subsect. *Bipartitae*, it is important to have an idea whether it is an ancient type or, morphologically, a more modern derivative. This hinges on the interpretation of the morphology of the inflorescences, especially that of the female sex.

Eichler accepted (41) the cupule of *Fagus* as having originated from four bracteoles; the cupular bracts he regards as emergences. Schacht,

¹ The manuscript of his paper on the New Caledonian species was finished in March 1953 and was submitted for the approval of his director, Prof. Däniker, Zürich.

² A similar shifting of the centre of genera caused merely by priority of description through the haphazard historical sequence of collecting has occurred in other South Pacific and Australasian genera, as in *Ascarina*, *Drimys*, *Vavaea*, *Faradaya*, and *Corybas*, and to a smaller extent in genera like *Trachymene*, *Oreomyrrhis*, and *Olearia*.

Celakovski (42, 43) and Prantl (23) accept the cupule as an intercalary hollow axial structure covered with reduced leaves ("Hochblätter") comparable with the inflorescence of a fig, though Prantl claims to have seen two bracteoles at the base of each cupule. Also Berridge (44) accepts the cupule as an axial structure with reduced leaves. Helmqvist equally (21, p. 86) recognizes its axial structure.

Miss Langdon, in her valuable study on the morphology of *Nothofagus*, comes to the (similar) conclusion (17, p. 365), that on the basis of vascular organization the cupular valves of *Nothofagus* may be interpreted as corresponding to the bracts and modified floral parts, including the axial portions, of the "tertiary units" of an originally more complex cymose inflorescence.

In the following I wish to disregard the question whether the cupule of all Fagaceous genera is homologous, and will limit myself to that of *Nothofagus*.

Broadly speaking, the character of the flowering parts is, in both sexes, that of a contracted, cymose inflorescence. This point of view is accepted by nearly all authors concerned save a single one who believes that the cupule is entirely an axial structure.

The appendages on the cupular valves of *Nothofagus* are by most authors accepted as representing "bracts" inserted on a lining of axial origin, but what kind of "bracts" are meant is not always clearly expressed.

In both sexes the flowers do not possess bracteoles. A bracteolate origin of the appendages is, therefore, not very probable.

Other "bracts" available are either the caducous perular "bracts" at the base of the flush or the stipules.

As in *Fagus*, the perular "bracts" are homologous with stipules. Like the latter they are inserted decussately, hence form four orthostichies and are provided with colleters at the adaxial base, but they are invariably basally attached. In various *Nothofagus* species with small basally attached stipules, the perular bracts do not differ much in shape or size from the stipules, though by contrast they never sustain flowers. In species with distinctly peltate stipules, however, perular bracts and stipules proper differ distinctly in size and shape.

The stipules are also inserted in four rows, orthostichies, as they accompany the alternate leaves on either side. They are firmly inserted and are more apt to have functioned in the formation of the cupule, as they are found apically of the perules. They also possess colleters. In the living species, ♂ flowers are never found in the axils of the perular bracts, but are often found on the leafless twig-base above the perular bracts sustained by the stipules.

It seems to me, therefore, that not the perular bracts, but the stipules proper, have taken part in the contraction of the ♀ inflorescence leading to the cupule.

A hypothetical Fagoidaceous ancestor of *Nothofagus* thus would have the following characters:

Male flowers in lateral cymose catkins at the base of the flush (in the

living species reduced to a triad or even a solitary flower, e.g., in 5. *N. pullei* and 7. *N. resinosa*, which both also show a remarkable parallel reduction in the ♀ sex!).

Female flowers in axillary prolonged catkins on lateral twigs provided with stipules but probably without leaves (as is sometimes the state of the basal part of the flush in living species).

Imagining a suppression of the length-growth of the female catkin-bearing twig and a simultaneous reduction of the basal catkins, the resulting ♀ inflorescence would be a crowded mass of stipules arranged in four orthostichies surrounding the terminal ♀ flowers of the upper catkins.

In this condensed inflorescence the stipules would still remain inserted on a base of axial origin, and these bases together would clothe the inner side of the then hollow (suppressed) twig with a coating of woody tissue of axial origin.

In this way four valves would result, capsule-like covering the ♀ flowers, each valve consisting of the inner lining of axial origin covered outside by the concrescent stipules, represented as "lamellae" in the living species.

It seems that only suppressed length-growth is needed for explaining the origin of the *Nothofagus* cupule.

Additional argument is derived from the presence of the colleters on the adaxial base of the lamellae in the living species. Also, the scarious apical part of the stipules is well reflected in the scarious nature of the lamellae in various living species. Another argument is the fact that the outer lamellae (representing the lowest stipules in the hypothetical ancestor) develop earliest in Papuan *Nothofagus*; the telescoping development of the lamellae could be well observed in 11. *N. bernhardi* (fig. 16c) where the very young cupule shows only one lamella, outside, concealing the inner ones, which are shorter but which gradually slide away from under the outer lamella.

The fact that the sexes in *Nothofagus* are separated agrees with the situation in other Fagaceae, Betulaceae, and allied families.

If this mode of origin of the cupule is accepted, there is little difficulty in correlating the morphology of the living species. I have presented this in a schematic construction in fig. 1.

A four-valved cupule with undivided scarious lamellae and containing at least three ♀ flowers is accepted as morphologically primitive both in sect. *Calucechinus* and sect. *Calusparassus*. The central (terminal) flower may be 2- or 3-merous.

In sect. *Calucechinus* the most primitive stage is found in *N. alessandri*, which normally possesses seven ♀ flowers in each cupule: one 2-merous flower is basal (central), the two lateral flowers are 3-merous and are inserted near the junction of the valves; besides, the base of each of the valves bears an additional 2-merous flower, so that apparently three cymes are represented. If we assume that the central (terminal) flower of each cyme is normally 2-merous in *Nothofagus*, this species even shows a tendency to a more complicated inflorescential design, viz., of five cymes, of which only in the basal one the lateral flowers are developed. Reduction

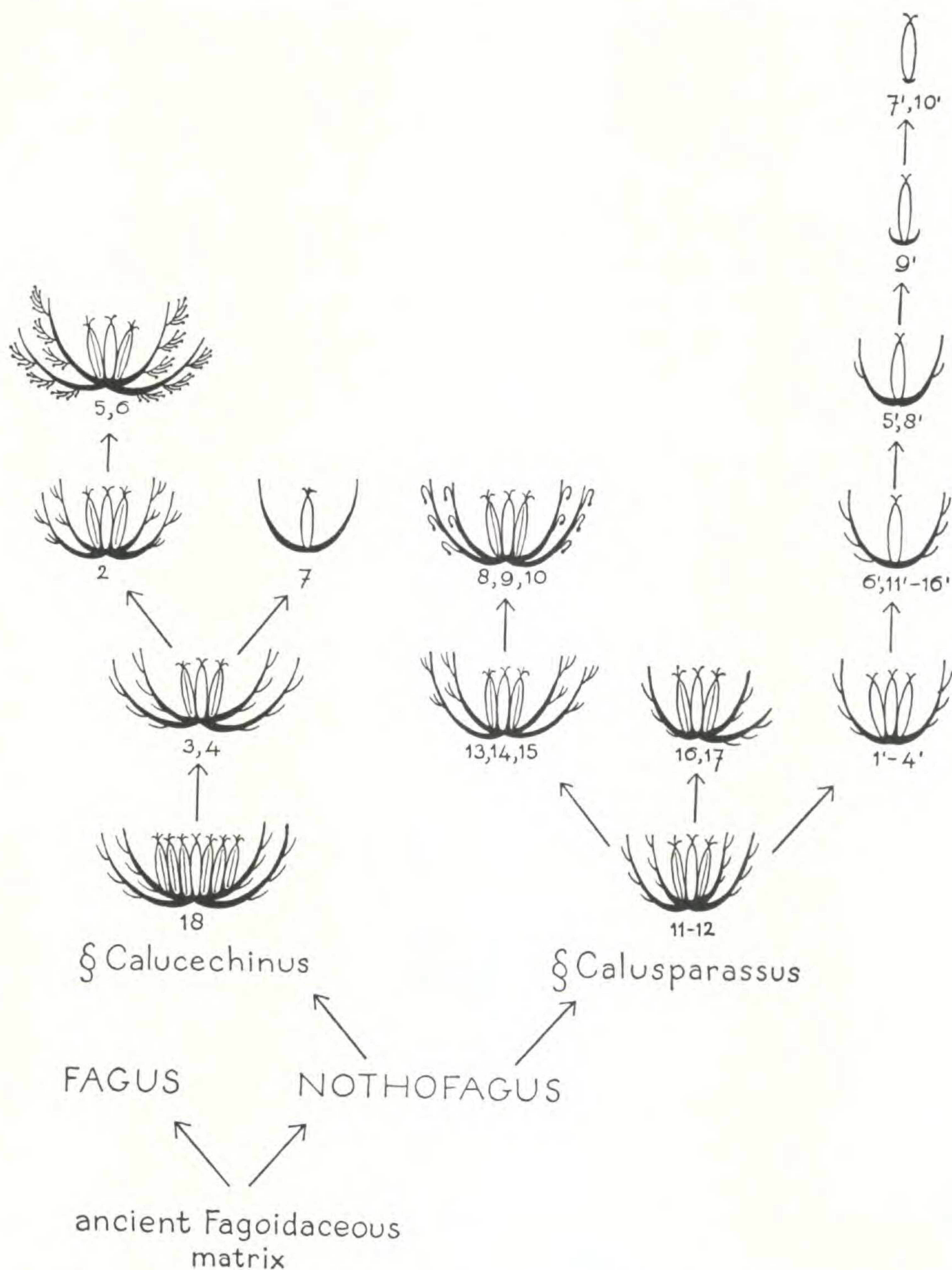


FIGURE 1. Scheme of morphological interrelations in the cupular structure of *Nothofagus*. Below each type the species referable to that type are cited by numbers corresponding with those of the key to extra-Papuan species. The numbers of the Papuan species (right column) correspond with those in their key and have been marked with an acute accent.

in number of female flowers leads to a 3-flowered cupule with entire lamellae. On the left side of the *fig. 1* there is a line leading to a further division of the cupular lamellae via species numbers 1 and 2 towards the intricate-fringed lamellae in species 5 and 6. On the other side there is a reduction of the lamellae leading towards further simplification of the valves by concrescence in pairs leading to the elamellar 2-valved cupule in species 7.

An argument for the possibility of concrescence of four valves into two has been found in some New Guinean 2-valved species with occasionally notched valves in the 2-valved species, e.g., in 2. *N. perryi* (*fig. 6e*).

An additional argument may be derived from the peculiar candelabra-shaped cupule of *N. glauca*, of which the flat basal part is broadened by the pairwise connate bases of the cupular valves through which these look forked. The lateral nuts are inserted at the junction of each fork, remote from the central flowers. Outside, the connate bases show a distinct furrow indicating the connation.

In sect. *Calusparassus* similar processes can be observed: reduction of valves and flowers on one side and ornamentation of the cupular lamellae on the other side.

Also here the most primitive morphology of the ♀ inflorescence is the one resembling that of sect. *Calucechinus*, viz., a 4-valved cupule with undivided lamellae and three ♀ flowers (in 14. *N. nitida* occasionally five ♀ flowers have been recorded!).

On the left side of the *Calusparassus* ancestry is a line leading towards cupules with intricate patterns of ornamentation brought about by a steady progression in the splitting of the cupular lamellae, which are split in spp. 13–15 followed by still more appendages, which are recurved and gland-tipped in spp. 8–10.

The other way round, viz., towards reduction, is found in the branch towards spp. 16 and 17, in which 3-valved cupules have been produced. As a matter of fact one of the three valves in these species is often broader than the two others and points to concrescence of one pair of valves into a single valve.

Another line of still greater reduction is the one on the right side of the scheme represented by the Papuan-New Caledonian species of series *Triflorae*, which are probably close to the ancient state in sect. *Calusparassus* save for their possession of exclusively 2-merous flowers (each probably representing the terminal flower of a cyme) and concrescence of four valves by pairs into two cupular valves. This leads easily to the species of series *Uniflorae*, where the number of flowers is reduced to a solitary one. And within this series *Uniflorae* a rather full series of four steps is observed leading to a still greater reduction of the cupule, which gradually loses its lamellae, resulting in the entire loss of the cupule in spp. 7 and 10.

That this tendency towards reduction is not wholly hypothetical is reflected in the fact that all of the species of series *Triflorae* possess triads of ♂ flowers, but that among the species with the most reduced cupules the male sex is also reduced to a solitary flower, viz., spp. 5 and 7.

Both tendencies, reduction of the cupular lamellae and progression in splitting of them towards more intricate ornamentation, are exhibited on the specific level. Concrescence of the cupular valves I assume to be representative of the subsectional level.

The discussion just given should be regarded as a cautious, subjective approach to a possible reconstruction of typological morphology. The interrelations were so obvious that I felt strongly invited to give some comment on morphological evolution. Unless the rather simple explanation of the origin of the cupule of *Nothofagus* is accepted, there is no possible way of explanation otherwise.

The species indicated as being illustrative of the different stages are illustrative only; it should not be concluded that I accept them as being the real way in which ancestral speciation has taken place in nature.

Nor should the relative age of the different stages of the scheme be regarded as a measure for the antiquity of the stages or species concerned. For it is quite possible that the physiological and morphological phenomena just accepted (suppressed length-growth of the inflorescence resulting in its condensation and reduction or ornamentation of cupular lamellae) have taken place during a relatively short geological period, giving the impression of having been performed simultaneously during early speciation.

Why such a peculiar reduction line is represented in New Guinea only I cannot tell, but I am satisfied that this line appears to be connected morphologically with the New Zealand 11. *N. fusca*. This fits in remarkably well with the plant geographic affinity of so many other Papuan mountain plants.

ECOLOGICAL REMARKS

As said above, *Nothofagus* is limited to a constantly cool and humid climate. It can stand even cold conditions, e.g., in South America, where its occurrence northward seems to be rather sharply demarcated at 33° SL, extending to only 35° SL in the Cordilleras, but not beyond the Aconcagua River, in the Argentine falling back to about 38° SL. Here two species of the deciduous section are found up to the timber line, according to Skottsberg (50), viz., *N. antarctica* on the west side of the Cordilleras in Chile and *N. pumilio* on the east side of the range above the former.

In South America *Nothofagus* stands occasionally seem to form the substage below *Araucaria*; it is noteworthy that the geographical area occupied by both genera is remarkably similar.

Also in New Zealand *N. cliffortioides* is found up to the timberline. In New Zealand some species show definite seed years in which fruit production is abundant, a remarkable parallel with European *Fagus*. In burnt forests saplings regenerate often freely, though repeated burning exterminates the *Nothofagus* forest (which is not fire-resistant) in favour of eucalypts in Tasmania and Victoria. The reverse proof of this balance is found in Queensland, where local *Nothofagus* stands or colonies dominated by *N. moorei*, sharply demarcated against surrounding forest types, seem

to encroach upon eucalypt stands to regain their natural climate-bound territory if burning practice is discontinued. According to Herbert (27), trees of *N. moorei* are often loaded with epiphytes; in some places regeneration is scarce, but elsewhere saplings are abundant.

Generally the southern beeches are typical dominants under optimal conditions.

The Third Archbold Expedition of 1938–1939 revealed the preponderant position which *Nothofagus* species occupy in the montane rain-forests of New Guinea. Mr. Brass earmarked most species as dominants or co-dominants in the fagaceous forests, in ground that was mossy or not mossy, in deep valley or slope forest, and in the mossy forest. The co-dominants may be other species of *Nothofagus* (as at Lake Habbema *N. decipiens* and *N. bernhardi*), or sometimes other montane tree species, as *Weinmannia urdanetensis*. The mossy condition does not make much difference in the botanical composition of the forest.

On ridges and crests the species of *Nothofagus* which in valley forest may attain lofty size (40 m. by over 1 m.) grow into stunted, gnarled brushwood 2–5 m. high. Species which are found under both conditions are 11. *N. bernhardi*, 5. *N. pullei*, and 1. *N. recurva*.

A similar dominant position is occupied by *Nothofagus* in New Caledonia, according to Dr. Baumann-Bodenheim. And this social behaviour is also found in extra-Melanesian species, as is well known from the southern beeches in Chile, the Argentine, and New Zealand.

The altitude at which *Nothofagus* is found in New Guinea ranges between 1000 and 3000 m., roughly coinciding with the montane zone distinguished by me (2), penetrating into the lower part of the subalpine zone. However, 90% of the collections have been made between 1750 and 2850 m. Only one species, notably that with the largest leaves, *N. grandis*, descends to lower altitudes, ranging from 1800 m. down to 900 m. (Bele River). The specimens found at the lowest altitudes were sterile.¹ There is a possibility that they were growing here below their potential minimum contour along watercourses.

The forest type in which Papuan *Nothofagus* occurs so gregariously is the tropical rain-forest, that is, the climaxal mixed evergreen forest under equatorial everwet conditions, i.e., the rainfall is about evenly distributed through the year without any marked or prolonged period of decidedly less rainfall. The mossy facies of many of these forests mark them as often having a constantly high relative humidity.

The gregarious occurrence becomes especially conspicuous when the reddish flush appears: Brass records of 11. *N. bernhardi* that the reddish young leaves tinge and characterize the forest in February. See further under 12. *N. grandis*.

As to the period of flowering, data on anthesis can best be obtained by summarizing the dates from the male flowering, as according to Schindler the period of anthesis is of very short duration; in 12. *N. grandis* he found it to last only one week. I have combined these dates and I find that the

¹ As is found in Java in seedlings of *Myrica esculenta* Buch.-Ham. (2: p. 336).

anthesis definitely coincides with the rainy season from October to March (one record being April 9). There is only one record definitely outside this period, viz., of 12. *N. grandis* which flowered at the end of July in the Madang district, but it is likely that the seasons are reversed here.

According to Mr. Brass 11. *N. bernhardi* is protandrous, which is in accordance with the sequence in which the flowers develop on the flush: ♂ flowers are always found below the ♀ ones, and may even appear in the upper axils of the perular bracts at the base of the twig. In several cases these ♂ and ♀ flowers are subtended by the young folded budstage leaf, but in several other cases there are no leaves subtending the flowers, which are then simply sheltered by the pair of large stipules. Thus in flush the flowers of both sexes are definitely exposed to the air. In proportion as the flush develops into normal-leaved branches the maturing of the fruit is inconspicuous and unexposed.

Pollination is apparently by wind, and each ♂ flower produces quite a quantity of pollen; the relatively large anthers bungle on the threadlike, hairy, long filaments and get often entangled. In many cases I found detached flowers or triads that had dropped as a whole. As several species may be co-dominant, the possibility cannot be excluded that by means of the wind such detached ♂ flowers may act as pollinating agents.

Dr. Skottsberg observed and photographed in New Zealand drifting pollen clouds, like smoke, above *Nothofagus* forest (cf. 8, p. 175, pl. 42a), like those above *Secale* in Europe. The windy climate of New Zealand, and doubtless of other regions in the roaring forties, causes this pollen to be widely spread by wind. This has been proved by R. Licitis (60). This author made an extensive study of air-borne pollen and spores in New Zealand, where the most abundant pollens are those of *Nothofagus* and grasses. Pollen masses of *Nothofagus* were found dispersed in the air far beyond the actual distribution of the trees, at least for a distance of fifty miles. The capture of pollen shows pollen shedding on peak days in definite periods between September and January, the highest percentage being shed apparently on the last fine day before rain.

Pollination conditions are such that hybrids can be expected, such as have been described from New Zealand by L. Cockayne c.s. (29, 30, 31, 32) and H. H. Allan (33). These polymorphic hybrids are referred to the progeny of crossings *N. fusca* × *N. cliffortioides*, *N. fusca* × *N. solandri*, and *N. truncata* × *N. solandri*.

Hybrids are equally well known from South America, especially in localities where stands of two species are close or overlap. They have been reported from Fuegia (*N. antarctica* × *pumilio*). Some authors assume *N. alpina* to be a hybrid (*N. procera* × *pumilio*). Dr. E. Kausel, to whom I am greatly indebted for essential information and material generously given on Chilean beeches, assumes the type tree of *N. leoni* to represent a rather intermediate hybrid (*N. glauca* × *obliqua*).

In nearly all species the innovations are more or less covered by a greyish or yellowish resinous layer during the flush period. This is apparently mainly exuded by the glands found near the insertion of the stipules, and

not by the numerous glandular punctate dots on the leaf surface itself. The immature cupules also appear sometimes wholly enveloped in resin, as in 3. *N. starkenborghi*, only the styles protruding into the free air. Part of this resin is probably produced by the sausage-shaped glands on the adaxial base of the lamellae. What the function of the resinous production is is difficult to tell. It could be imagined that it is a protection of the sexual organs against frost, but on the other hand anthesis occurs (in Papua) during the rainy season when no frost is likely to occur in the montane zone.

Also protective action could be imagined in the ecupular, very resinous 7. *N. resinosa*, the ovary of which might need protection, but resin production should then be equally abundant in other ecupular species like 5. *N. pullei*, which is not so, and no resin would be needed in 3. *N. starkenborghi*, where the cupules are found to be very resinous.

Also in the rainy season there is no urgent need for protecting the innovations against undesirable desiccation. Therefore I have abandoned the idea of a direct relation between resin production and climatic conditions.

Mr. Brass, in his field notes, has remarked on an occasional possible dioecism of some Papuan *Nothofagus* species. This has been taken over by Miss Langdon (17). The sheets referred to were in young fruit and beyond anthesis. And I assume the caducous male inflorescences had disappeared at this stage. In some cases I still found some spare, detached, old ♂ flowers caught in a twig fork or stuck in a place where some resin was left, e.g., behind a stipule. I am not sure whether these ♂ flowers belong to the same tree, as the triad may have been brought by wind from other trees. Pending additional field data, I accept all species of *Nothofagus* as monoecious.

The gregarious occurrence of *Nothofagus* supposes an abundant production of fruit and subsequent seedling reproduction. As a matter of fact I found many cupules, defective and unripe ones, attacked by animals, some of which are apparently fond of the nuts. A similar observation was made by Dr. Baumann-Bodenheim in New Caledonia. This damage is probably caused by small seed-eating birds. Reiche (19) says that the nuts are often sterile in South American species. The large nuts of *N. glauca*, which equal those of *Fagus sylvatica* in size and shape, will probably be palatable to man. In New Zealand there are marked seed years. Both in South America and New Zealand and in New Guinea mature nuts are produced about half a year after pollination.

Nothofagus forest appears to be valuable to man. In Mr. Brass' opinion Upland Papuans have mainly made their fields on the soils bearing fagaceous forests: man has followed the beeches, he says. That the trees are well known to Papuans, partly on account of their suitability as timber-producing plants, appears from the fixed native names, which in East New Guinea are apparently "generic" names, such as "ufoiya" and "ifoya" (resp. in the Anona and Aiyura dialects), further, "gripe" (Schindler), "sama" (Brass), and "unuza" (Kamano dialect, Womersley). Father

DuBuy of the Sacred Heart Mission, Ononge, who materially helped Mr. Brass in establishing friendly relations with the turbulent Papuans of the Mt. Albert Edward and Mt. Tafa areas, has used 2. *N. perryi* timber in building his mission.

PARASITES OF NOTHOFAGUS

It would have been interesting if Papuan *Nothofagus* had been accompanied by typical parasites which have been described from extra-Melanesian species.

There is a notable genus *Cyttaria* (Discomycetes), of which seven species are known to be confined to *Nothofagus*, according to Prof. D. A. Herbert (9). He collected a new species on the border of Queensland and New South Wales on *N. moorei*, the northernmost known locality of the genus *Cyttaria*.

More than one species of *Nothofagus* may be attacked by the same species of fungus, while the same beech may be parasitized by more than one species of *Cyttaria*. The fungus causes big galls covered by gelatinous stromata; branch growth is retarded and its distal parts may be killed. In a dry atmosphere the stromata become leathery. Simpson and Thomson report *Cyttaria* as the greatest opponent to the forest growth of *N. menziesii* in New Zealand (10).

Darwin, in his Journal of Researches, mentioned *C. darwinii* of Tierra del Fuego as being eaten uncooked in its mature state, a delectable article of food of Araucarian Indians. Also the Tasmanian *C. gunnii* was eaten by aborigines and was known to the settlers as tree morel. Prof. Herbert found the Queensland species quite palatable. In New Zealand W. C. Davies (26) stated *Cyttaria* to be a favourite food of the native New Zealand pigeon, *Hemiphagus novae-Zelandiae*.

Recently Dr. Santesson (11) wrote a beautifully illustrated revision of *Cyttaria*. As he says that *Cyttaria* is entirely confined to *Nothofagus* as its host-tree and that it follows *Nothofagus* in its whole distributional area, it might be expected to occur in New Guinea and New Caledonia. In the material I examined I could, however, find no gall-like deformations which might be ascribed to *Cyttaria*. As *Cyttaria* is less common in Australasia than in South America, and the Queensland species was only very recently and locally found, it is certainly to be expected to occur in New Guinea. Special attention should be paid to its occurrence by those privileged to explore Papuan *Nothofagus* forests. Altitudinally *Cyttaria* does not seem to have preference.

Heim (63) gave a brief account of the mycological flora of the southern beech forest.

Another peculiar parasitic genus confined to *Nothofagus* is *Myzodendron*; this, however, is not homotopical, as it is confined to South America, according to Dr. Skottsberg (12, 13).

A few species of *Nothofagus* possess domatiae, i.e., hair-tufted pits in the

axils of the primary nerves. These are found in *N. menziesii*, according to Cheeseman (39); they are also recorded in *N. fusca*. Poole says (38, p. 365): "domatiae have always been found in *N. fusca* on trees and saplings above 2–3 m. On seedlings and saplings below this height they are usually not present." Du Rietz (18) gave some comment on the occurrence of domatiae in these New Zealand species. I have not been able to find additional domatia-bearing species. Espinosa (54) mentions hairs in the nerve axils of *N. leoni* from Chile, a feature which I could verify. Similar hairs are present along the equally subhirsute midrib in *N. glauca*, and traces of insects are present in specimens of both species. These domatiae are not so distinct as in the New Zealand species. Domatiae also occur in *Fagus* species and in *Quercus* species.

It is often assumed that these domatiae are due to acari and that they are to be considered as gall-like structures in which acari find a shelter. As a matter of fact, empty skins of acari are often found between the domatial hairs, and I found them in *Nothofagus*. In many cases the occurrence of domatiae is used in taxonomy for specific distinction. No experiments are known to me to verify whether domatiae are a normal morphological character or are due to a teratological growth caused by the acari. As a matter of fact Reiche (19, p. 419) mentions from Chile that acari cause densely hairy spots on the undersurface of leaves and that Neger identified certain *Erineums* in *N. dombeyi* and on *N. obliqua*. In both species, however, domatiae are absent. The above-mentioned fact, that in very young seedlings of *N. fusca* no domatiae are found, is not proof that they represent malformations caused by acari.

Also in zoocecidiae *Nothofagus* has some peculiar associates, and several remarkable galls are found which have been described by Houard (49). He says that the galls on southern beeches "rappellent aucunement celles du *Fagus sylvatica* de l'hémisphère boréal."

Among Papuan specimens I found two gall-bearing numbers, viz., of *N. brassi* (Brass 11103) and *N. carri* (Carr 15028) which I turned over to the well-known cecidologist Prof. W. M. Docters van Leeuwen. Though the material is very scarce he is prepared to accept them as psyllid galls. A similar gall I found in *N. truncata* from New Zealand. Psyllid galls are common to tropical mountains but have never been found in northern *Fagus*.

EVALUATION AND VARIATION OF CHARACTERS

Habit and size: Little distinctive value can be attached to habit and size for taxonomical purposes, as both show a great phenotypical plasticity through response to external factors. On exposed stony crests and the mossy scrub of ridges 1. *N. recurva*, 5. *N. pullei*, and 11. *N. bernhardi* grow stunted and shrublike, but may attain great size on deeper soils in sheltered places on lower slopes and in valleys of New Guinea. In New Zealand a similar behaviour is recorded for *N. solandri* and in South America for *N. antarctica* (50, p. 108) and *N. pumilio* (50, p. 104).

The twigs: Little distinctive value can be found in the twigs which are terete; in single coarse species, as 2. *N. perryi*, they are somewhat flattened near the nodes. In many species they are slightly zigzag, as is often found in distichous alternate leaves. The only Papuan species which has hairy twigs is 5. *N. pullei*. The hairiness in extra-Papuan species tends to disappear with age.

The perules: The axillary perules are in some species small, but in others, especially the coarse-leaved ones, they are rather distinct; their size, of course, varies with the season. The densely imbricate, decussate bracts are ovate to triangular (with the exception of *N. moorei*, *N. procera*, *N. alessandri*, and *N. leoni*), in contrast to those in northern *Fagus*, and they are placed in four distinct orthostichies. When the flush appears they are mostly early caducous. They are often slightly varnished; on their adaxial base they possess sausage-shaped resin-exuding colleters which are placed in a transverse row.

This tallies with the occurrence of similar colleters found on the base of the stipules and proves that the perular bracts represent stipules. This conforms to the situation in *Fagus*, in which Büsgen (55) mentions the same (except the two lowermost, which represent reduced leaves).

The perular bracts are always basally attached, and though they telescope a little during the growth of the flush, the scars which they leave are found crowded at the base of the lateral twigs. On the base of the twig in flush, the lowest genuine stipular pairs are sometimes found continuous with the upper perular bracts and may bear ♂ flowers (cf. fig. 22c).

The basal part of the perules is always thicker than the blade, which flares out membranously; the basal part is thickened to an abnormal degree in *N. gunnii*.

The stipules: It is peculiar that mention of the stipules is seldom found in descriptions of the southern beeches. Often it is recorded only that they are caducous or deciduous. Sometimes they seem to have been confused with the perular bracts.

I find that they present marked additional specific characters (fig. 2).

In the Papuan species they are always distinctly peltate, which is comparable to the situation in several of the Chilean species of sect. *Calucechinus*, and their insertion is surrounded by concentric rings of sausage-shaped resinous glands. In 5. *N. pullei* they remain for a very long time on the twigs, but in most species they are early caducous after the flush has matured. At the insertion there is outside mostly a knob-like thickening. Their shape in Papuan species is always oblong to roundish, and though they are somewhat smaller in some species than in others, I have not used their shape or dimension for determination. Cf. fig. 4b, 5b, 7b, c, e, g, 8d, 10b, c, 12b, c, 14b, 15b, 16b, 17b, 20c, e, 21b, 22b.

This is definitely different in extra-Melanesian species (cf. fig. 2); *N. antarctica*, *N. betuloides*, and *N. pumilio* possess stipules like the Papuan species, *N. fusca* has very narrow, peltate stipules of which the basal part is smallest and emarginate; *N. dombeyi* has ovate stipules of which the

part below the insertion is narrow; *N. obliqua* has similar but hardly peltate stipules; and *N. solandri*, *N. cliffortioides*, *N. gunnii*, *N. cunninghamii*, and *N. menziesii* have stipules which are not peltate, the resin glands being placed in a semicircle or row along the apical part of the insertion. But again they vary in shape: in *N. gunnii* they are small and

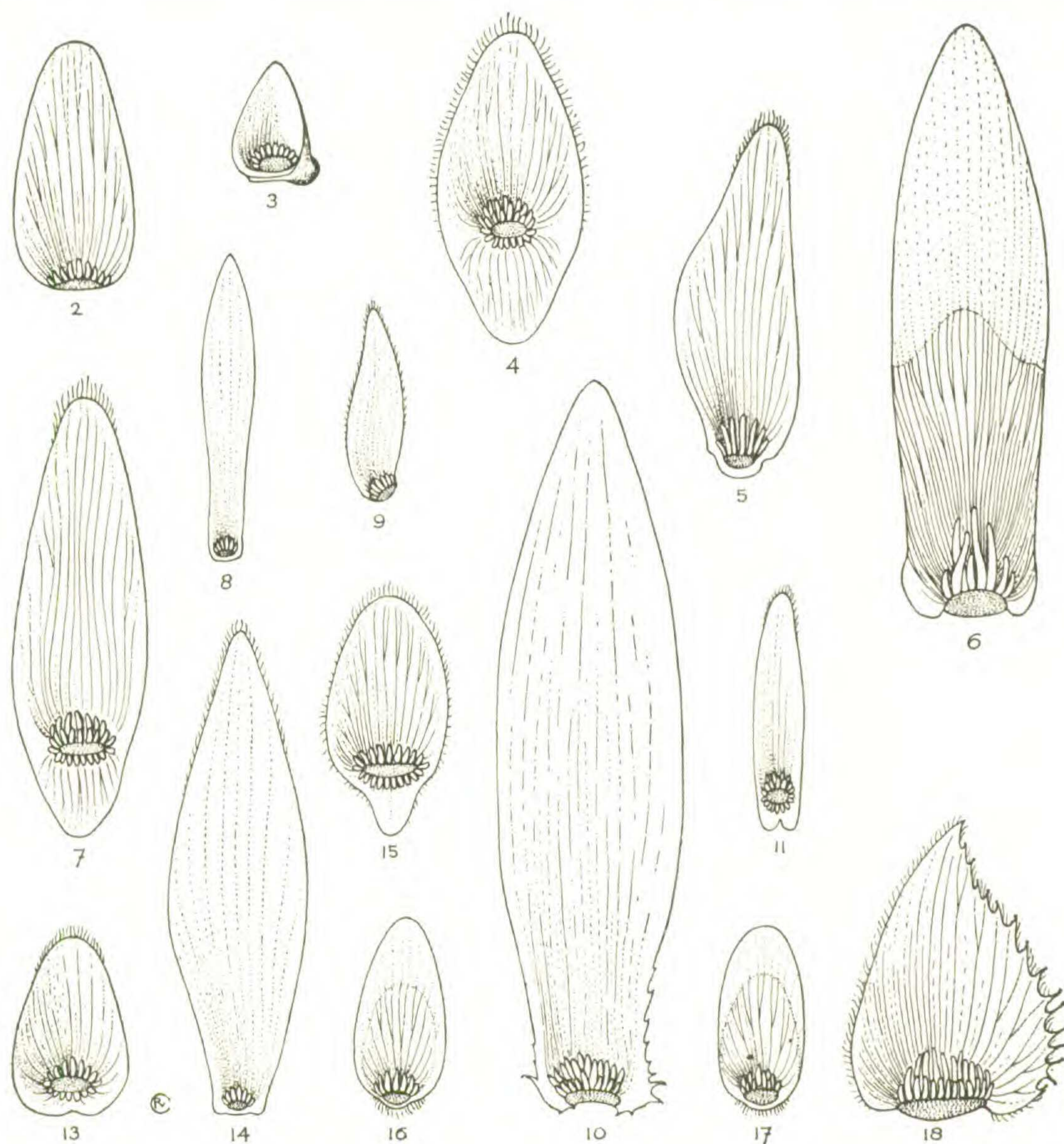


FIGURE 2. Stipules of extra-Malaysian *Nothofagus* species, the numbers corresponding with those in the key: 2. *N. obliqua*, 3. *N. gunnii*, 4. *N. antarctica*, 5. *N. alpina*, 6. *N. procera*, 7. *N. pumilio*, 8. *N. menziesii*, 9. *N. cunninghamii*, 10. *N. moorei*, 11. *N. fusca*, 13. *N. betuloides*, 14. *N. nitida*, 15. *N. dombeyi*, 16. *N. solandri*, 17. *N. cliffortioides*, 18. *N. alessandri*. — All $\times 7$.

triangular and with a strongly thickened basal saccate portion like the leaf-base of a *Sedum*; in *N. cliffortioides* they are narrow-oblong, more or less boat-shaped; in *N. menziesii* very narrow-triangular; in *N. solandri* they are elliptic; and in *N. obliqua* bluntly triangular.

As I have explained elsewhere, I regard these stipules s. l. as the organs

from which the cupule is condensed, being homologous with the lamellae of the cupule, the inner part of which I assume to be of axile nature: a very much condensed "hollow" split twig with a condensed inflorescence.

Unfortunately the structure of the stipules does not yield characters suitable for infra-generic distinction.

The leaves: There is great variation in the leaves of *Nothofagus*, the greatest difference being between the deciduous, almost always thin-textured leaves of sect. *Calucechinus* with plicate vernation, and the persistent, flat, always coriaceous or at least firm leaves of sect. *Calusparassus*, which in bud are not plicate but flattish or folded-convex; Papuan species are consistently folded along the midrib, exposing their undersurface. In all species the innovations are varnished by resin which is partly exuded by the stipules, which mature much earlier than the leaves, and partly by the dermal, lepidote glands on the leaves themselves. In New Guinean species the very young leaves are often covered with a thick resin film. This resin is not soluble in alcohol, only partly so in turpentine, but wholly soluble in ether and acetone. The older leaves show, generally, a less varnished surface. The physiological action of this exudation is obviously associated with the flush period.

The distinctness of the glands in herbarium specimens varies rather widely and depends on the age of the leaves and on the stage of the tree from which the specimens were collected, physiological action of the glands being strongest during the flush period.

At the base of the shoot the lowest nodes often bear only stipules; between them sometimes no trace of a reduced leaf is found, but in other cases I found a tiny appendage obviously representing a much reduced leaf. It is remarkable that the upper leaves of a flush mature earlier than those lower down (cf. *fig. 7b, 12a*).

The midrib is prominent below and sulcate on the upper surface, but in all Papuan species a thin ridge runs along the centre of it on the upper surface, continuing on to the petiole. In *N. starkenborghi* there is only a groove without midrib tissue visible; here the ridge is found only on the petiole.

The spacing of the punctate-dotted glands, which are best observed on the undersurface of the leaves, is somewhat different in different species. Glandular dots on the leaves are different in number and size in different species; I have the impression that more than one type of gland occurs.

Nervation in the coriaceous Papuan species is not strongly prominent except on the undersurface. The nervation pattern and especially the way in which the nerve ends are looped or branched in connection with marginal teeth and crenations seem to differ considerably from species to species. A fossil form genus, *Parafagus*, has been based solely on this character of curved nerves branching off near the margin to a lower tooth. In *fig. 3* I have made a picture of the very different patterns of nervation of several living species from different sections and series. This might be of use to palaeontologists.

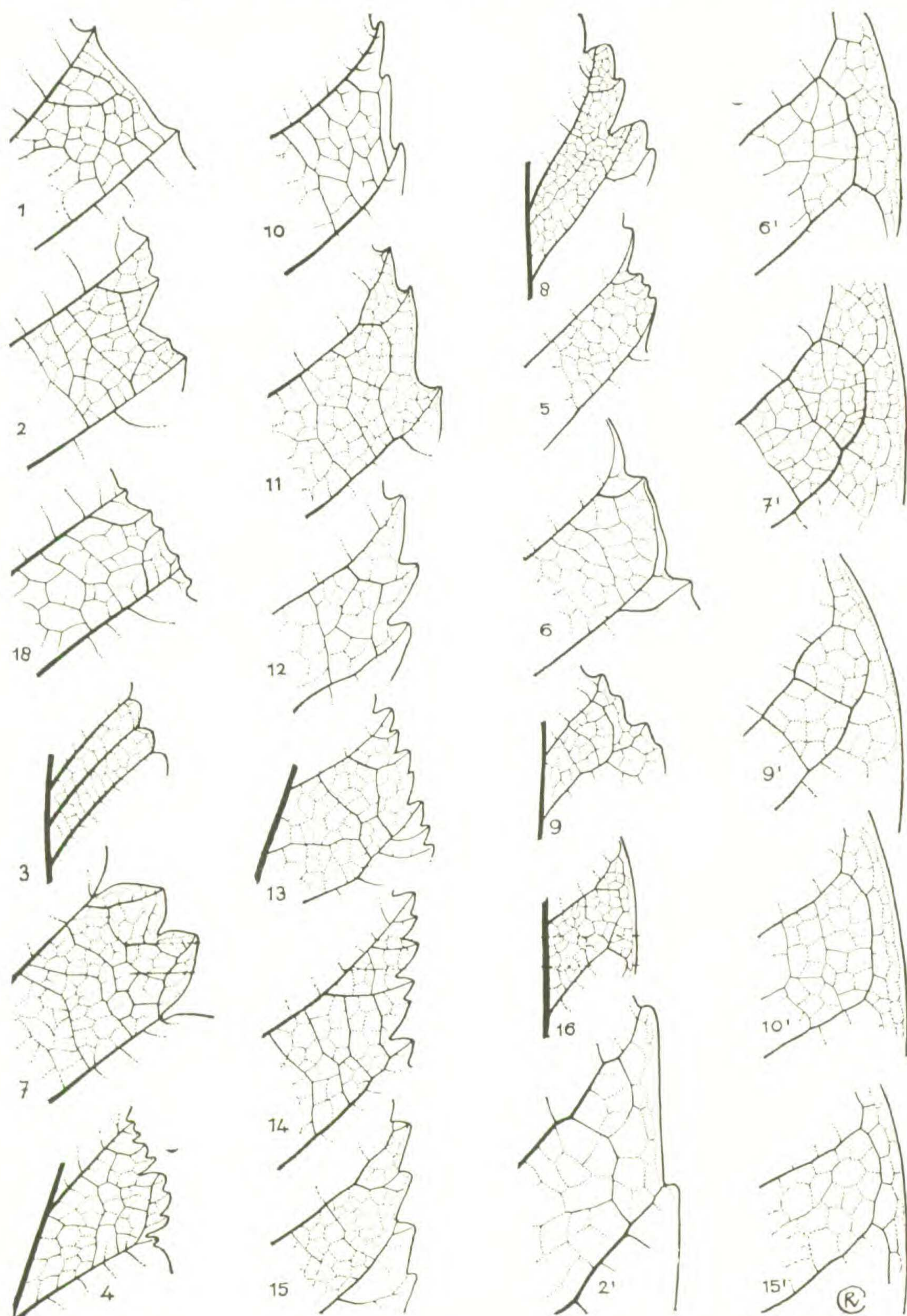


FIGURE 3. Types of nervation in *Fagus* and *Nothofagus*, the numbers corresponding with those in the key; the Papuan species marked with an accent. To be compared in the following sequence: — 1. *Fagus sylvatica*, 2. *Nothofagus obliqua*, 18. *N. alessandri*, 3. *N. gunnii*, 7. *N. pumilio*, 4. *N. antarctica*, 10. *N. moorei*, 11. *N. fusca*, 12. *N. truncata*, 13. *N. betuloides*, 14. *N. nitida*, 15. *N. dombeyi*, 8. *N. menziesii*, 5. *N. alpina*, 6. *N. procera*, 9. *N. cunninghami*, 16. *N. solandri* (same as *N. cliffortioides*), 2'. *N. perryi*, 6'. *N. crenata*, 7'. *N. resinosa*, 9'. *N. carri*, 10'. *N. cornuta*, 15'. *N. eymae*. — All $\times 3$.

From *fig. 3* it appears clearly that the nervation pattern is rather different within the genus.

In *Fagus sylvatica* and some species of *Nothofagus* the primary side-nerves run straight and directly to the margin (in spp. 1, 2, 18, 3, 8, 5, 9). In others they do the same but give off a more or less distinct lower curved vein to a lower marginal tooth (spp. 4, 10–15). In all these cases the leaf margin is toothed or crenate, and the teeth and crenations are distinctly served by nerves or thicker veins ending in the margin.

This is distinctly different in all species which have entire leaves, viz., *N. solandri* and *N. cliffortioides* (*fig. 3: 16*) and the Papuan species (*fig. 3: 2'–15'*). They show distinctly looped side-nerves which do not end in the margin. It seems that the condition of the margin is bound to the nervation pattern.

Nothofagus cunninghami (*fig. 3: 9*) occupies more or less an intermediate position between the first and third type, its open nervation showing a tendency to become looped.

As I had never thought about a correlation between these two “characters” I have looked into some other genera embracing toothed and entire leaves. Rather to my astonishment I found a similar correlation of entire leaves with looped nerves and toothed leaves with open nervation in several other genera, viz., *Viburnum*, *Gynura*, *Eupatorium*, and to a certain extent in *Osmanthus*, and some *Ficus*. In *Viburnum luzonicum* both combinations are found, even within one species (Kern, in Reinw. 1: 164. 1951). In other genera, e.g., *Evonymus*, other *Ficus*, *Ilex*, and *Symplocos*, the looped nervation is not or is only slightly affected by the marginal condition.

I wonder whether this correlation is more or less physiologically connected with the nerves serving marginal teeth for secretory function in certain stages of the ontogeny.

Palaeontologists working with leaf imprints should be on the alert in evaluating these characters.

It is satisfactory that species which are close in the key show a similar nervation, e.g., in the group *N. alpina*–*N. procera* (*fig. 3: 5 & 6*) where the nerve curves upwards along the margin. There is no nervation difference between *Fagus* and *Nothofagus*; the latter genus displays a greater number of nervation types than the former.

Reticulations are often closely netted, especially in the coriaceous species, the leaves of which show a tessellate surface, e.g., in *N. solandri* and several small-leaved Papuan species. In all *Nothofagus* the areoles seem to contain a blind vein.

The cartilaginous leaf edge in Papuan species is mostly entire, but a few species have crenate-dentate leaves. The leaf margin is very often recurved, and sometimes the leaf is distinctly convex; in others, however, it is distinctly flat. The leaf-tip is always notched.

In some extra-Malaysian species domatiae have been found in the axils of the primary nerves which have been studied by Du Rietz (18), but in none of the Papuan species have I found a single indication of them. I

observed them also in Northern hemisphere *Fagus sylvatica*, *F. ferruginea*, and *F. sieboldii*.

In many *Nothofagus* species the leaf shape furnishes a good specific character. The leaf size is often also to some degree rather constant. It is sometimes held that southern beeches are all microphyllous, which would make quite a contrast to the Papuan representatives. In the first place some of the Papuan species are microphyllous, and among the extra-Papuan ones several possess moderate-sized or large leaves, as *N. procera*, *N. obliqua*, *N. alessandri*, and *N. glauca* and their hybrids. The New Caledonian species possess large leathery leaves. The leaf surface is seldom hairy; in New Guinea this condition is found only in *N. pullei*. In *N. recurva* I have distinguished a microphyllous variety, but not in *N. grandis*, though here also the leaf size is rather different, which might be due partly to age, exceedingly large leaves being found on manifestly old twigs.

It is quite possible that besides distinctive specific characters, the cuticle structure may yield additional characters for a subdivision of the genus. Miss Cookson has made a tentative promise to perform this anatomical research initiated by Miss Bandulska (57).

The petiole in Papuan species is semi-terete; its flat upper surface often bears a marginal ridge, and along its centre the continuation of the midrib ridge is found. The petiole appears in some species to be slightly lepidote, but I assume this is due to traces of resin scales from the flush period.

The male flowers: Male flowers are inserted axillary on the flush, always below the female flowers. In Papuan species they seemingly appear sometimes from the upper perular bracts, but really they are placed between the lowest efoliate stipules. They are essentially placed in triads, occasionally five ♂ flowers have been found in *N. fusca*; the triad is often incomplete and reduced to two or one flower. There are no bracteoles. The shape of the tube and limb are rather variable, but will be found useful locally for furnishing differential characters.

In several Papuan species the tube is narrowed at the base into a hypanthial basal part.

In the Papuan species the limb is closed in bud and is torn apart by the growing anthers (fig. 4c). In several other southern species the limb is neatly (valvately) lobed, and the tube is either rotate or campanulate. In the Papuan species the tissue is glandular-punctate, and this will hold essentially for the other species.

The stamens vary considerably in number, but within certain limits they seem rather constant for the species. The size and shape of the anthers also provide characters. In many Papuan species the stamens are distinctly punctate-glandular to warty-glandular.

The filaments in northern *Fagus* are free from the base. This is also found in several southern *Nothofagus*; in *N. obliqua* and *N. dombeyi* they are slightly connate. During the lengthening in anthesis the bases of the filaments of several Papuan *Nothofagus* appear to be connate in a distinct basal column.

In some Papuan species the filaments are straight in bud (*fig. 4c', 20d'*), in others, however, they are serpentine folded (*fig. 14d*). In all species the anthers are exserted; in the herbarium it is difficult to judge to what final degree. In the Papuan species the filaments are finally mostly very long, and the relatively large anthers bungle far out of the flower in a typical anemophile way. As the filaments are mostly hairy, they often get entangled.

As on each flush the male flowers appear earlier than the female ones, the flowering appears protandrous. The ♂ anthesis is of only a few weeks' duration, after which the flower or triad falls off as a whole, by which the twig may give the impression of being female. There is no question, however, that *Nothofagus* is dioecious, as is assumed by Helmquist (21, p. 82).

The female inflorescences and flowers: The female inflorescences are axillary; after anthesis cupules which appear originally sessile or subsessile may show a distinct peduncle.

In some Papuan species the lowest ♀ inflorescences are clasped by efoliate pairs of stipules (*fig. 12f*).

The valves of the cupule are free from the beginning or connate to various degree, in some Papuan species even forming a cup. In the herbarium cupules open also when still immature.

At the base of the lamellae resinous colleters are found. The lamellae themselves are very varied in shape, entire or split into horizontal, inverted-V-shaped or curved rows of appendages, and are often good differential characters. The appendages themselves may be entire or fringed (*N. procera* and *N. alpina*), and they are often gland-tipped. In one Papuan species the lamellae appear to be absent (*fig. 14c*); this condition is also ascribed (wrongly) to *N. montagni*. In two Papuan species the cupule is absent, and the solitary female flower is embraced solely by the stipules (*fig. 12f, 15b*).

The growth of the lamellae is distinctly centripetal, and in flower it sometimes appears that the inner lamellae are wholly concealed by the outer one; they subsequently telescope from behind one another (*fig. 16c*).

The female flowers are inserted at the base of the cupule; judging from the scars in fruit they appear somewhat tortuous in the three-flowered species by mutual pressure. In principle the central flower appears to be 2-merous, the laterals 3-merous. If the cupular valves are narrow the wings of the lateral flowers may fit in neatly between the valves, but in other cases they are pressed in various ways. In a single species, *N. glauca*, from Chile, the lateral 3-merous flowers stand distinctly apart through the pairwise connation of the basal part of the valves: the lateral nuts are here remote from the central one and stand candelabra-like upright, each clasped by the free apical portions of two valves.

In *N. alessandri* seven flowers are closely packed; the central flower is 2-merous, the two lateral flowers are 3-merous; besides there is one 2-merous flower attached to the base of each of the four valves.

Occasionally the number of nuts per cupule differs, e.g., in *N. solandri* one, two, or three, but usually there are two in that species.

The perianth of the ♀ flower is connate to the ovary wall but forms wings along the margins by which the apical limb is often produced above the style base as a shoulder. In a single Papuan species two other lobes of the limb are hornlike, produced from the sides of the flower (*fig. 15c*). In *N. pumilio* according to Helmqvist (21) coalescence of ♀ flowers is found sometimes, resulting in a 3–7-winged perianth.

In 2-merous species the ovary is 2-celled, in 3-merous species 3-celled, corresponding respectively with two and three styles and two and three wings on the flower.

Each cell contains two apical hanging ovules, but only one ovule develops into seed; the dissepiments disappear. In many cases the fruits in the herbarium are wholly sterile, though the pericarp is well developed. A similar situation is found in European *Fagus*, where many fruits are barren.

The vascular tissue in the dissepiment leading towards the ovules is distinctly developed and appears in fruit as a false funicle. This vascular tissue may be forked in the upper part, each fork feeding two ovules.

The fruit: Properly this is morphologically an achene and not a nut. Its morphology is essentially similar to that of *Fagus*. Still it is common usage to call it a nut, and this has been followed here. The pericarp and perianth tissue develops horny and is glabrous inside in contrast to *Fagus*. In ripe seeds one still finds the abortive ovules at the apex of the seed near the attachment of the false funicle. Cotyledons are distinctly folded and contain fat reserve instead of starch, as in *Fagus*. The hypocotyl develops at the apex of the seed, splitting the pericarp (*fig. 18d, e*).

Poole (38, p. 503) speaks about the parthenocarpic development of fruit; he found growth of the fruit without pollination. However, no seed was formed in his experiments.

The setting of the fruit appears both in southern *Nothofagus* and in Papuan species to take about half a year. Reiche (19, p. 400) found in *N. obliqua* that germination occurred two months after the seeds had been placed. Germination is epigeic. According to Dr. Kausel, the fully developed cotyledons of seedlings are subreniform in *N. glauca*, *N. obliqua*, and *N. procera*.

GENERIC DIFFERENCES BETWEEN FAGUS AND NOTHOFAGUS

Though at present *Fagus* and *Nothofagus* are generally regarded as distinct genera, it seems worth while to list their generic characters:

Fagus	Nothofagus
Perulae elongate, very acute; bracts without colleters.	Perulae roundish to ovate, very rarely elongate; bracts with colleters at the adaxial base.
Stipules never peltately inserted.	Stipules mostly peltately inserted but the basal wing sometimes narrow or reduced.

Stipules ligulate, flaccid, firmer towards the apex.	Stipules very rarely ligulate, scarious towards the apex.
Stipular insertion not surrounded by sausage-shaped resinous colleters.	Stipular insertion surrounded by sausage-shaped resinous colleters.
Leafblade not glandular-dotted.	Leafblade distinctly punctate-glandular dotted.
♂ flowers in long-peduncled, globular, many-flowered, hanging inflorescences.	♂ flowers sessile to short-peduncled, solitary or in triads.
Anthers not apiculate, eglandular.	Anthers apiculate, often glandular.
Pollen with 3 furrows.	Pollen with 5 or more furrows.
Cupular appendices irregularly placed, without resin glands.	Cupular wings or appendices distinctly lamellar, very often with resin glands and basal adaxial resinous colleters.
♀ triad normally without a central flower.	♀ triad always with a central flower, lateral flowers sometimes reduced.
Styles elongate, tip papillose.	Styles short, stigmatic arms papillose over their length.
Nut sharp-angled but not winged.	Nut generally winged.
Endocarp hairy. ¹	Endocarp glabrous. ¹
Wood rays several cells wide.	Wood rays 1-2 cells wide.
Wood fibres with bordered pits.	Wood fibres with simple pits.

Few comments are needed on this table. Solereder (22) was originally responsible for the data on the differences in wood structure. He examined several species; his distinction was confirmed for eleven additional species examined by Krasser (36, p. 161). See also the figures by Mouranche (62) and Wagemann (67) who made an extensive anatomical study of Chilean *Nothofagus*.

According to Metcalfe & Chalk the wood of *Fagus* and *Nothofagus* is most closely allied within the Fagaceae (47).

The character of the narrow or broad rays is possibly of less value than it seems, as it is said that in both *Pasania* and *Quercus* broad and narrow rays seem to occur in one genus.

Yatsenko-Khmelevsky (from 47, p. 1314) studied the wood of *Nothofagus* and concluded that it diverged very early from related genera and that the wood of its most primitive representatives probably resembled that of *N. cunninghami*.

The glandular nature of *Nothofagus* is also expressed in several species with punctate-glandular dotted stipules, ♂ perianths, and distinct glands on the anthers.

The pollen character has been advanced by Miss Cranwell (8) and has been further elaborated by Miss Cookson (4, 5, 45).

¹ Not tested in all species.

SUBDIVISION OF THE GENUS *NOTHOFAGUS*
WITH A KEY TO THE SPECIES

Among those interested in the *Nothofagus* problem there has temporarily been a feeling that the Papuan and New Caledonian species should represent a new genus, distinct from *Nothofagus*. It is true that they possess a pollen type of their own, and the wood is slightly different from that of other *Nothofagus*. Also the leaves, especially in the New Caledonian species, are generally larger than those of the South Pacific.

However, Miss Cookson, who has unrivaled knowledge about *Nothofagus* pollen, maintains that their pollen definitely is that of a *Nothofagus*, and she quite agrees with an infra-generic status of the Papuan-New Caledonian taxon.

The same view is held by Prof. I. W. Bailey, who, in Dec. 1939, on invitation of Dr. E. D. Merrill, made some anatomical research on Papuan *Nothofagus*. His notes, contained in two letters, were kindly put at my disposal. He wrote: "The pollen of the new plants are typical of *Nothofagus*. The general structure of the stamens and anthers likewise resembles *Nothofagus*. Furthermore, in clearing the leaves for study, I note that both sets of leaves yield a similar reddish pigment. When one takes into consideration the structure of the bark, of the nodes, of the xylem, of the pollen, etc., it seems to me that one should proceed with considerable caution in setting up a new genus. It seems to me that a new section of the genus *Nothofagus* is all that is warranted by the evidence that I have examined. In fact the structure is just about what one would expect in a species of *Nothofagus* from a tropical montane habitat."

A similar view is held by Miss Langdon in her valuable detailed account of the anatomy (17).

To gain an insight into the structure of the genus and the characters which may lead to a subdivision of the genus I have also studied extra-Papuan species, though by no means intending to monograph the whole. It appears that the characters common to all species are many and essential; the taxon is a very coherent one.

Several attempts have been made to subdivide it, even though it was originally included in *Fagus*. Mirbel (24, p. 472) divided the genus *Fagus* into two groups, one with plicate leaves (incl. *Fagus* s. str. and *N. obliqua*) and one with nonplicate leaves, and though *Fagus* s. str. has later been split off from the first group, the essence has been to keep the vernation character as the main point. Mirbel was followed in 1840 by W. J. Hooker (28), in 1847 by Endlicher (34), in 1864 by A. de Candolle (16), in 1871 by Oerstedt (15), who was the first to treat *Nothofagus* species in the present circumscription, in 1883 by Solereder (22), in 1896 by Krasser (36), in 1897 by Reiche (19), in 1947 (to a certain extent) by Miss Langdon (17), by myself (14), and by Miss Camus (61).

As said above, De Candolle fitted the deciduous, plicate-nerved *Nothofagus* species into *Fagus* subgen. *Eufagus*, which included thus both

northern and southern hemisphere beeches. This was corrected by Bentham & Hooker (35), who accepted *Nothofagus* as a section, cf. Blume's circumscription of 1850, under *Fagus*.

In 1842 another generic name had been proposed by Spach (64), viz., *Fagaster* Spach, typified by "Fagus dombeyi et quelques espèces voisines, indigènes de l'Amérique australe; ces végétaux diffèrent des vrais Fagus, principalement par leur involucre, qui est partagé en lanières étroites, ne recouvrant point les noix." Phytographically this description is that of a *nomen semi-nudum*, but formally we cannot avoid taking it into consideration for priority. No specific combinations were made by Spach. The name is proposed here as a *nomen rejiciendum*.

Two other generic names were proposed for *Nothofagus* in the Atlas Bot. Dicot. of the voyage of the "Astrolabe" and "Zélée" by Hombron & Jacquinot,¹ viz., *Calucechinus* Hombr. & Jacq. for the deciduous species and *Calusparassus* Hombr. & Jacq. for the evergreen ones.

Pritzel states that this Atlas was published in 1853, and this date is also printed on the title page. However, it is certain that the Atlas (or parts thereof) was distributed at a much earlier date. As early as 1846 Lindley (Veg. Kingd. 291) mentioned both generic names *Calucechinus* and *Calusparassus*, and both were cited a little later by Walpers (Ann. 1: 636. 1848-1849) with exact reference to the details of the plates. In cases such as this one never knows whether the author(s) have occasionally distributed manuscript copies or proof sheets to befriended colleagues who, with or without permission, have used these for their own works.

This is, however, not the end of the story. Additional data were provided most liberally by Mr. W. T. Stearn of the British Museum in a letter dated June 4, 1953. Mr. Stearn says that in ascertaining the publication dates of these French Voyages many difficulties arise from the fact that the publishers often issued a livraison of plates, without text, in an undated or even wrongly dated wrapper. According to B. D. Jackson, who consulted a copy of the questioned Atlas having the wrappers preserved (cf. Jour. Bot. 26: 269-272. 1883), the plates were issued in thirteen livraisons between 1844 and 1853. Unfortunately the wrappers themselves were not dated. Also it is not known exactly how the Atlas was issued, whether each part separately, or occasionally in issues containing more than one part.

The plates concerning *Nothofagus* are Phan. Dicot. 6, 7, and 8. It appears that plate 6 (wrongly lettered "Monoc.") was issued in livr. 6, and plates 7 and 8 in livr. 8. The latter was acquired by the British Museum on Jan. 17, 1845, and may have been issued in 1844, but livr. 6 was not acquired by the British Museum until 1853. Apparently it was "missed in publication" and was acquired later to complete the work. This plate also was probably issued in 1844 or 1845, since Walpers was acquainted with it by 1849.

For the validity of the generic names *Calucechinus* and *Calusparassus*

¹ Decaisne, who wrote the text of the vascular plants of this work (1855) cites only Hombron's name; he did not accept the two proposed generic names, reducing them to *Fagus*.

it was of paramount importance to know whether livr. 6 had appeared before livr. 8 or whether they appeared simultaneously, or whether livr. 8 had appeared earlier than livr. 6. In both latter cases the genera would not have been proposed as monotypic and should be neglected for purposes of priority.

However, Mr. Stearn found a review (in Hooker's London Jour. Bot. 3: 128. 1844) which establishes conclusively that livr. 6, containing tab. 6 (*Calucechinus antarctica* and *Calusparassus forsteri*), appeared before livr. 8, as the latter, containing tab. 7 & 8, was reviewed later in the same serial (l.c. 4: 28. 1845).

Hence, both generic names take their publication as to the names of monotypic new genera from tab. 6 (1844) and *Nothofagus* must be conserved against them, which is here accordingly proposed.

In 1858 Turczaninow (37) described a fruiting specimen from Chile as a new genus of the Sapindaceae, viz., *Lophozonia heterocarpa* Turcz.

In 1940 Dr. Hatusima collected with Prof. Kanehira a species on Mt. Arfak, West New Guinea, accepted by him to represent a new genus of the Hamamelidaceae allied to *Distylium*, but in 1943 he agreed with me that it was a *Nothofagus*; Miss Langdon (17, p. 353) wrongly stated that this hamamelidaceous genus, the name of which was found on herbarium labels, had been published during the war in Java.

Though W. J. Hooker, in 1840, and Oerstedt, in 1871, had given keys, no infrageneric taxa were described until Krasser (36) gave a comprehensive survey of the genus in 1896, a work which unfortunately escaped my attention when publishing the preliminary note (14).

Krasser's main aim was to study differential characters between *Fagus* and *Nothofagus*, for which he mastered the literature and made some anatomical and taxonomical research, which he concluded by giving a conspectus. This contains several new infrageneric epithets and seven new binomials antedating Reiche's transfers by one year. There is nothing new in his division, it is entirely based on that given by Oerstedt, but his names have been considered and taken care of. Some were as yet not entered in Index Kewensis and have been overlooked by later authors. Mr. Bullock affirms their validity.

Among the fossils of New Zealand quite a few *Nothofagus* species have been described from the Tertiary. Rather recently Oliver (48) described several new species of *Fagus* and *Nothofagus*, and even a new (form) genus, *Parafagus*. He based his work mostly on the nervation and the way in which nerves end in crenations along the margin. This new genus is distinguished mainly by the curved nerves, but these are found equally in the New Guinean species. It is quite possible that *Parafagus* is a straight synonym of subsect. *Bipartitae*, as pollen grains conformable to those of the living Papuan species have also been found in New Zealand. According to the drawing in Oliver's paper, the fossil New Zealand *Parafagus otakonia* Oliver is almost an exact replica of the living Papuan *N. perryi* Steen. Among living *Nothofagus* there are several types of nervation as shown in fig. 3, so that there is no place for a distinct genus *Parafagus*.

based only on this character. I reduce it to *Nothofagus*, but will refrain from transferring the species described under fossil *Fagus* and *Parafagus* to *Nothofagus*. If I had living leaf fragments in a state comparable to those fossil leaf imprints for identification, I should strongly advise the wastebasket as their proper disposition.

In the deciduous species the leaves are plicate in bud along the lateral nerves (as in *Fagus*) and are later soft in texture (with a single exception). In the evergreen species they are not plicate but are either flattish or (as in all New Guinean species) folded along the midrib, pressing the upper halves against each other and exposing the undersurface.

As to the cupule, the Melanesian group possesses 2-valved cupules, a character shared by *N. pumilio* from South America, which also has only one 3-merous ♀ flower. However, this species does not seem closely related to the Melanesian ones, as it possesses deciduous, plicate leaves.

All other species possess 4-merous cupules, two New Zealand species with 3-merous cupules excepted.

As to the ♀ flowers of the Melanesian species which are consistently 2-merous, it is noted that in the southern species with 3-merous flowers the central flower is also nearly always 2-merous. There is, though, some individual variation, as the lateral flowers are in single cases also, one or both of them, 2-merous. I also sometimes found all three flowers 3-merous.

Independently of Reiche (19), I have come to the conclusion that the number of ♀ flowers of the cupule represents a constant character, though of less value than the structure of the cupule.

As to the ♂ flowers, there is quite a variation, but the androecium appears to me unimportant for infrageneric value. The Papuan species all have typically tubular perianths; in several southern species these are more campanulate or even wider in shape, but this character, with the number of ♂ flowers (one or three), and the number of stamens in each flower — which is rather constant for each species and ranges between about (5–) 8 and 40 (–90) — is too irregular to serve for infrageneric distinction.

After long considering the desirability of subdividing the genus, thereby making a *lapsus calami* in wrongly typifying one of the sections (14, p. 146) and making it still worse by a clumsy, superfluous attempt to correct this error (14, p. 316), moreover, overlooking Krasser's paper, I have come to the conclusion that the characters do not warrant a distinction of subgenera, only of sections and minor divisions. Interrelationships appear to be reticulate in several cases. It is out of the question that more than one genus is represented.

It remains to be seen how far this division of the genus is also reflected in anatomical characters (wood, epidermis, pollen). That the Papuan-New Caledonian species deserve a special taxon on the basis of anatomy has already been made clear by Miss Cookson and Dr. Dadswell.

It would have been very welcome if the differences in structure of the pollen of *Nothofagus* had wholly coincided with its morphological characters. This is, however, only true to a certain degree. Miss Cranwell (8)

distinguished in New Zealand *Nothofagus* two types, viz., the *menziesii* type and the *fusca* type. This is sustained by Miss Cookson for pollen of living Australian species (4, 5). She found both types also among the fossil pollens. The *menziesii* type includes *N. menziesii*, *N. cunninghami*, and *N. moorei*, which are also found close together in my key, but also the deciduous *N. obliqua*. And the *fusca* type embraces in addition to the evergreen *N. fusca*, *N. truncata*, *N. solandri*, *N. cliffortioides* also the deciduous *N. gunnii*, which I regard as a taxonomically remote species, as well as the majority of South American species of which several are deciduous. Therefore it seems to me that the pollen type is not a good criterion for taxonomic infrageneric distinction.

It would have been equally welcome if an infrageneric grouping of all species could be made on wood-anatomical characters. This may be promising, as according to Dr. Dadswell the species of subsection *Bipartitae* appear to be mutually close and differ from other *Nothofagus*. Dr. Dadswell was even inclined to regard this subsection as of higher rank. A forthcoming paper on the subject by Dr. Dadswell will certainly be of great interest, especially if it contains data on many southern species.

Taxonomically it has never been endeavoured to correlate the species into infrageneric taxa with a single key to the representatives of different countries. Though a monographic treatment falls outside the scope of this study, I feel that such a provisional conspectus may be useful. Unfortunately, some types have been unavailable, and also I could not obtain in time material of two newly described Chilean species.

The difficulties in identifying types are greatly extended by the fact that of the about twenty extra-Melanesian species no less than eight have been based on completely sterile material, while six others were typified by sheets in which only one sex was represented.

However, I have some hope that in general the structure of the key and the main distinctive characters will be acceptable. In several cases I have expressed a provisional opinion about specific delimitation.

Quite a number of misidentifications have not been accounted for here; I have limited myself to the interpretation of type names.

Of some species many varieties have been distinguished, e.g., in *N. antarctica*; these minor varietal names have not been included. Also names of hybrids have been omitted.

Summarizing, this key to extra-Melanesian species should be regarded as a first attempt towards a provisional basis for future work.

Nothofagus Blume,¹ Mus. Bot. Lugd.-Bat. 1: 307. 1850; Oerstedt, in Vidensk. Selsk. Skr. ser. 5, 9: 354. 1871; Prantl, in Engler & Prantl, Nat. Pfl. Fam. 3, 1: 52. 1893, nom. conserv. propos.

Fagaster Spach, Hist. Nat. Vég. Phan. 11: 142. 1842, nom. rejic. propos.

Calucechinus Hombr. & Jacq., in Dumont d'Urville, Voy. Pol Sud & Oc. (Astrolabe & Zélée) Bot. Atlas, Dicot. t. 60. 1844; t. 7Z, 8II. 1845, nom. rejic. propos.

¹ No binomials were proposed by him under *Nothofagus*.

Calusparassus Hombr. & Jacq. l.c. t. 6Σ. 1844; t 7Γ, 8Ψ. 1845, nom. rejic. propos.

Lophozonia Turcz., in Bull. Soc. Imp. Nat. Moscou 1858, 1: 396. 1858.

Fagus subg. *Calusparassus* Miq., Ann. Mus. Bot. Lugd.-Bat. 1: 103. 1863.

Fagus subg. *Calucechinus* Miq., l.c.

Fagus sect. *Eufagus* A. DC. in DC., Prodr. 16, 2: 117-123, pro parte, pro spp. 4-8.

Fagus sect. *Nothofagus* A. DC., l.c., emend. Benth & Hook. f., Gen. Pl. 3: 410. 1880.

Nothofagus subg. *Lophozonia* Krasser, in Ann. Hofmus. Wien 11: 162. 1896.

Nothofagus subg. *Molischia* Krasser, l.c.

Parafagus Oliver (gen. foss. Nov. Zel.), in Trans. & Proc. Roy. Soc. New Zeal. 66: 292. 1936.

Deciduous or evergreen, glabrous or short-hairy, perular, trees or shrubs. Innovations generally varnished by exuded resin. Bracts of the perules in four orthostichies, at their adaxial base with resinous colleters. Leaves distichous, alternate, in bud either folded along the midrib exposing either their inner or outer surface or flattish or plicate along the lateral nerves, entire or variously toothed or crenate, thin or firm in texture, with lepidote, resinous punctate-dotted glands, tip mostly emarginate; midrib flat or sulcate, in the Papuan species sulcate and provided on the upper surface with a fine, prominent ridge, at least at the base, or if a midrib is invisible on the upper surface this ridge is distinct on the petiole; veins reticulate, areolae with a blind vein. Petiole semiterete, margins often elevated. Stipules often large, roundish to linear, mostly distinctly peltate, provided on the adaxial side around the insertion with mostly several rows of radiating resinous colleters, often soon caducous, sometimes long-persistent. Flush appearing from the perules; nodes often leafless at the base, or with a rudiment of a leaf between the stipules. ♂ flowers at the base of the flush, axillary, sometimes between foliar stipules, solitary or in triads, sessile to short-pedicelled or short-peduncled. Perianth closed in bud, later splitting rather irregularly or valvately lobed, often glandular dotted, lower portion often constricted. Stamens (5-) 8 to about 40 (-90), filaments either free or with their base more or less connate into a column, in bud straight or more or less serpentine-rolled, at first short, later exerted, during anthesis sometimes much elongated, threadlike. Anthers mostly linear, sometimes oblong, basifixed, often glandular, 2-celled, cells splitting lengthwise laterally, connective apiculate. ♀ inflorescences axillary, sessile to short-peduncled. Cupular structure 2- or 3- or 4-valved, connate to various degree, sometimes the valves almost free; valves consisting of an inner woody lining bearing lamellae which may be entire or are split to various degree into often glandular-tipped appendages and often bear colleters on the adaxial side mostly near the base; in some cases a cupular structure is reduced. ♀ flowers solitary or in triads, rarely 7, middle flower generally 2-merous, lateral flowers either 2- or 3-merous (sometimes one lateral flower reduced), all sessile and inserted at the base of the cupule, in a single species a solitary 3-merous flower. ♀ flower with a 4- or

6-merous perianth connate to the ovary resp. fruit, mostly forming wings along the fruit. Ovary 2- or 3-celled, each cell 2-ovuled. Style rather short, often subpersistent; stigmas 2 or 3, papillose over their surface. Ovules anatropous, hanging from the top of the dissepiment, distinctly connected with the base of the ovary by a threadlike bundle of vessels in the central part of the dissepiment; this bundle sometimes forked in its upper part; only one ovule per fruit developing into a seed; dissepiments disappearing in fruit. Nut (achene) more or less distinctly winged, one-seeded. Endocarp not hairy inside. Seed exalbuminous, hanging from the top of the hardened vessel-bundle, of which the apex is still provided with the 3-5 abortive ovules. Testa membranous. Cotyledons thin, folded, with fat reserve. Germination epigeic, the hypocotyl possibly appearing on top of the fruit as in *Fagus*.

Species about forty, in temperate South America, Fuegia, Falkland Islands, and other South Pacific subantarctic islands, New Zealand, Tasmania, Victoria, New South Wales and South Queensland, New Caledonia, and New Guinea.

I. Sect. **Calucechinus** (Hombr. & Jacq.) Krasser, in Ann. Hofmus. Wien 11: 163. 1896.

Calucechinus Hombr. & Jacq. in Dumont d'Urville, Voyage Pol Sud & Oc. Bot. Atlas, Dicot. t. 60. 1844; 7Z. 8II. 1845.

Lophozonia Turcz. in Bull. Soc. Imp. Nat. Moscou 1858, 1: 396. 1858.

Nothofagus subg. *Lophozonia* (Turcz.) Krasser, l.c. 162.

Nothofagus sect. *Deciduae* Steen. in Blumea 7: 146. 1952.

Nothofagus sect. *Plicatae* Steen., l.c. 306, laps. cal.

Leaves deciduous, plicate in bud, texture almost always thin. — LECTO-TYPE: *N. antarctica* (G. Forst.) Oerst.

DISTRIBUTION: South America to Tasmania.

Subsect. 1. **Antarcticae** subsect. nov.

Cupula 4-partita, 3-flora. — TYPE: *N. antarctica* (G. Forst.) Oerst.

DISTRIBUTION: South America to Tasmania.

1. Lamellae entire or appendages simple and short.
2. Lamellae split into or provided with flat, erect or slightly recurved, simple, sometimes gland-tipped appendages. ♂ flowers solitary; stamens 20-90. Leaf-margin duplicate-serrate.
3. Cupule to 1 cm. peduncled, 20-25 mm. long. Lamellae 2 or 3. Lateral (trigonous) nuts 15-16 × 10 mm., not winged though with a marginal ridge. Stamens 40-90. Basal part of the cupule deeply split, flat, narrow, the lateral nuts leaving a semilunar scar below the lanceolate, acute-acuminate valves proper, the whole candelabra-shaped, scars ca. 1.5 cm. apart. Valves proper ca. 2 cm. long, 5-6 mm. broad at the base. ♂ flower 1 cm. pedicelled, perianth flattened, densely short-pubescent. Anthers hairy at the apex. Leaf underside glaucous, petiole (ca. 5 mm.) and undersurface of midrib hirsute, leaf-axils appearing bearded. Blade 4.5-8 × 3-5 cm., base subcordate, nerves ca. 10 pairs, straight, nervation open. Bark papery. *Fagus glauca* Phil., *N. megalocarpa* Reiche. Mts. of Central Chile

[Prov. Santiago (Cerros de Aculeo) to Prov. Nuble].

1. *N. glauca* (Phil.) Krasser.
3. Cupule subsessile to 3 mm, peduncled, 5–8 mm. long, short-hairy, lamellae 4–6. Nuts 5–6 mm. long (or in var. *macrocarpa* DC. to 10 mm.), distinctly winged. ♂ perianth subglabrous, pedicels puberulous. Stamens 20–40, anthers glabrous. Leaves elliptic-oblong, 2–5 cm. long, base generally cuneate, subglabrous, nerves 8 or 9 pairs. *Fagus obliqua* Mirb., *Fagus valdiviana* Phil., *Lophozonia heterocarpa* Turcz. Chile, The Argentine.
2. *N. obliqua* (Mirb.) Oerst.
2. Lamellae entire.
 4. Leaves ovate-oblong, base broadly rounded to subtruncate, 5.5×3.5 to 13.5×8 –9 cm.; nerves 11–13, parallel, straight, ending unbranched in the finely dentate margin. Stipules hairy, either auricled or not at the base. ♂ flowers in triads, short-pedicelled, with 10–20 exserted stamens. Cupule short-peduncled, hairy, 10–13 mm. long, 7-flowered; valves 9 – 11×4.5 –5 mm., with 5–7 lamellae. Nuts 6.5–7.5 mm. long. Chile (Mts. of Prov. Talca and Maule, according to Dr. Kausel). 18. *N. alessandri* Espinosa.
 4. Leaves much smaller, with fewer nerves. Cupular lamellae 3–4; valves subglabrous. Cupules much smaller, with 3 ♀ flowers.
 5. Leaves distinctly bullate-plicate, roundish-ovate, 1–1.5 cm. diam., marginal crenate incisions coinciding with the ends of very regularly parallel primary nerves. Twigs short yellow-hairy. Cupule 8–9 mm. long. Lower perular bracts and stipules with a strongly thickened saccate base. *Fagus gunnii* Hook. f. Tasmania. 3. *N. gunnii* (Hook. f.) Oerst.
 5. Leaves roundish ovate to oblong, often sub-lobed, 1.5–4.5 cm. long, margin with more than 2 teeth between the less regularly parallel primary nerves. Lower perular bracts without a very thickened base. Cupule ca. 5–7 mm. long. Stipules thin, oblong, very peltate. Nucular wings not shouldered but ending at the style base, ciliate towards the apex. ♂ flower with 8–13 stamens. *Fagus uliginosa* Phil., *Fagus antarctica* Forst., *Calucechinus antarctica* Hombr. & Jacq., *Calucechinus montagni* Hombr. & Jacq.,¹ *N. montagn(e)i* Reiche. Chile, The Argentine. 4. *N. antarctica* (Forst.) Oerst.

1. Lamellar appendages fringed to multifid, fringes gland-tipped.

6. Nuts high-shouldered, hairy especially at the top. Cupular bracts with an intricate pattern of rather thickish appendages. Leaves 2 – 3×1 –1.5 cm. *Fagus alpina* Poepp. & Endl. The status of this species needs further study. Chile. 5. *N. alpina* (Poepp. & Endl.) Oerst.
6. Nuts high-shouldered. Cupular valves with long, pinnately fimbriate, green, gland-tipped, thin appendages. Leaves 4–12 cm. long, oblong, blunt, not undulate. *Fagus procera* Poepp. & Endl., *Fagus nervosa* Phil., *N. nervosa* (Phil.) Dimitri & Milano.² Chile, The Argentine.
6. *N. procera* (Poepp. & Endl.) Oerst.

¹ This was figured with lamellar cupular valves; Reiche accepted it wrongly as elamellar.

² Index Kewensis listed an earlier *Fagus procera* Salisb. Prodr. Stirp. 391. 1796 (= *Castanea sativa* Mill.) which Dimitri & Milano (25, p. 7) accepted to have priority

DUBIOUS

19. *Nothofagus leoni* Espinosa, in Rev. Chil. Hist. Nat. 30: 268. 1926; ibid. 32: 175–187, t. 8, 9, fig. 31–37. 1929.

This is, according to Dr. Kausel's most instructive information, a natural hybrid between *N. glauca* and *N. obliqua*. Dr. Kausel examined both the type specimen and additional material of the original tree from which it was obtained. It has several features in common with *N. glauca*; the bark shows a little of the remarkable papery structure of the latter but does not peel. The cupules possess four rows of lamellar appendages and appear intermediate, as are the leaves. The nuts are larger than in *N. obliqua* var. *macrocarpa* (10–13 mm.) but smaller than in *N. glauca* and are distinctly winged as in *N. obliqua*. The tree is located in a region where both *N. glauca* and *N. obliqua* occur and where their areas overlap. Mr. Wagemann who knows the type-locality very well told Dr. Kausel that there are only 8–10 individual trees of *N. leoni* known to occur.

It is quite possible that this hybrid is identical with *N. obliqua* var. *macrocarpa*, but the latter might also represent a separate species. Additional collections are necessary to clarify this point.

Subsect. 2. **Pumiliae** subsect. nov.

Cupula 2-partita, valvae lineares. Flos ♀ unica, 3-mera. — TYPE: 7. *N. pumilio* (Poepp. & Endl.) Krasser. *Fagus pumilio* Poepp. & Endl., *Calusparassus pumilio* Hombr. & Jacq.

DISTRIBUTION: Chile, The Argentine.

NOTE: This has been reduced by some authors to *N. antarctica* but appears to me quite apart. Cf. also Philippi, Linnaea 33: 237. 1864; Reiche, in Verh. Deut. Wiss. Ver. Santiago de Chile 3: 409. 1897.

The leaf margin shows two teeth between the primary nerves; the latter are appressed-hairy on the lower surface, and the midnerval zone is often haired on the upper surface. This regular nervation is not found in *N. antarctica*, in which the dentation incision is principally the same but double-crenate. The regular nervation reminds one of *N. gunnii*, which, however, has only a single internerval tooth.

II. Sect. **Calusparassus** (Hombr. & Jacq.) Krasser in Ann. Hofmus. Wien 11: 163. 1896.

Calusparassus Hombr. & Jacq. in Dumont d'Urville, Voyage Pol Sud & Oc. Bot. Atlas Dicot. t. 6Σ. 1844; t. 7Γ. 1845, pro parte.

Nothofagus sect. *Sempervirentes* Steen. in Blumea 7: 146. 1952.

Nothofagus sect. *Planae* Steen., l.c. 306, laps. cal.

over *Fagus procera* Poepp. & Endl. Mr. Forman, Kew, was so kind as to copy Salisbury's reference for me. It appears that "procera" was merely an indication of its habit but not a specific epithet; even if this interpretation should not be accepted, it is a superfluous *nomen nudum* given in synonymy, which, hence, cannot be used for purposes of priority.

Leaves persistent, not plicate in bud but flattish or folded along the midrib exposing the undersurface or the upper surface, with firm texture. — LECTOTYPE: *N. betuloides* (Mirb.) Oerst.

DISTRIBUTION: South America to Queensland and Melanesia.

Subsect. 3. **Quadripartitae** Steen., l.c.

Cupule 4-parted, lamellae subentire to lobed, parted or divided into appendages. Lateral ♀ flowers normally 3-merous. — TYPE: *N. betuloides* (Mirb.) Oerst.

DISTRIBUTION: South America to Queensland.

1. Fruiting cupular valves with several lamellae each bearing or presenting a row of recurved, linear, glandular-tipped processes. ♂ flower solitary.
 2. Leaves roundish, under 2 cm. long, with few coarse teeth or crenations. Cupule 5–6 mm. long. Stipules 2–4 mm. long.
 3. Fimbriae arising from rather decidedly scale-like lamellae. ♀ perianth hornlike produced far above the top of the carpel, wings acuminate, in the sinus with spinous processes. Leaf underside with at least 2 basal domatiae; leaf margin thick, texture thick. *Fagus menziesii* Hook. f. New Zealand. 8. *N. menziesii* (Hook. f.) Oerst.
 3. Appendages flatter, horizontally attached from less decided scale-like lamellae. ♀ perianth not reaching above the top of the style, wings bluntish without spinous processes in the sinus. Domatiae absent, texture and margin less thick comparatively. *Fagus cunninghami* Hook. f. SE. Australia, Tasmania. 9. *N. cunninghami* (Hook. f.) Oerst.
 2. Leaves ovate-oblong, acute, (1.5–) 3–6 (–11.5) cm. long, serrate. Cupule 8–10 mm. long. Stipules 1–1.5 cm. long, reflexed. Lamellae several, attached in inverted V-shape pattern. *Fagus carroni* C. Moore, *F. moorei* F. v. M. South Queensland and New South Wales 10. *N. moorei* (F. v. M.) Krasser.
1. Fruiting cupular valves not with such regular lamellar rows of recurved, linear, glandular-tipped processes. ♂ flowers 1–3.
 4. Cupule with 2–4 entire or shortly ciliate lamellae on each valve; valves rather broad-ovate, pubescent.
 5. Leaves with 4 or 5 pairs of primary nerves, the margin on either side with 6–8 deep acuminate teeth. Domatiae present. *Fagus fusca* Hook. f. 1840 p.p., em. 1854, pro Hook, Ic. Pl. t. 631. New Zealand 11. *N. fusca* (Hook. f.) Oerst.¹
 5. Leaves with 5 or 6 pairs of primary nerves, leaf margin with 8–12 shallow blunt teeth. Domatiae absent. *Fagus truncata* Colenso. *Fagus fusca* Hook. f. p. p., Hook. Ic. Pl. 630. *Fagus fusca* var. *colensoi* Hook. f. 1854. New Zealand. 12. *N. truncata* (Colenso) Cockayne.¹

¹ Cockayne, whose specific distinctions are followed here for the New Zealand species (as extracted from Poole's work, lit. 38) regards *N. blairii* (Kirk) Krasser and *N. apiculata* (Colenso) Krasser as belonging to the hybrid groups formed between *N. fusca* and other species.

The difference between *N. fusca* and *N. truncata* as given by Poole (38, p. 370–371) is not very convincing for a specific status of these two species, as it is practically limited to vegetative characters.

4. Lamellae provided with one or two tooth-like erect appendages (laciniae); valves narrow, glabrous. Leaves glabrous, serrate. Twigs hairy.
6. ♂ flowers solitary, pedicelled. Stamens 10–16, filaments exserted. Leaves ovate-elliptic. This and the following two species are apparently closely related. *Betula antarctica* (Forst. Comm. Goett. 9: 45. 1789, nom. nud.) Willd. Sp. Pl. 4, 1: 466. 1805. *Fagus betuloides* Mirb. 1827, *Fagus dubia* Mirb. 1827, *Fagus forsteri* Hook. 1840, *Calusparassus betuloides* et *C. forsteri* Hombr. & Jacq., *N. patagonica* Gandoger. Chile, The Argentine. 13. *N. betuloides* (Mirb.) Oerst.
6. ♂ flowers in triads. Leaves ovate-lanceolate, acutish, 2–3 cm. long. Cupular valves on the back with short tooth-like appendages.
7. ♂ flowers with 5–8 stamens; pedicels yellow-hairy. Leaves ovate-oblong-triangular, $2.25\text{--}3.5 \times 1.25\text{--}2$ cm., in sicco brownish. Nerves and veins at the leaf-base fanned-subtriply-nerved. Filaments as long as the perianth. *Fagus nitida* Phil. Chile, The Argentine. 14. *N. nitida* (Phil.) Krasser.
7. ♂ flowers with ca. 8–15 stamens, triads peduncled. Filaments exserted. Cupular valves shorter than the nut. Leaves ovate-oblong to ovate-lanceolate, $2\text{--}3 \times 0.75\text{--}1.5$ cm., in sicco mostly greenish yellow. *Fagus dombeyi* Mirb. Chile, The Argentine. 15. *N. dombeyi* (Mirb.) Oerst.

Subsect. 4. **Tripartitae** subsect. nov.

Cupula 3-partita, lamellae indivisae, lamina integra, supra tessellata, infra tomentosa. — TYPE: *N. solandri* (Hook. f.) Oerst.

DISTRIBUTION: New Zealand.

1. Leaves blunt.¹ Flowering cupule 2×1.5 mm., very hairy. Tall, at low altitude. *Fagus solandri* Hook. f. New Zealand. 16. *N. solandri* (Hook. f.) Oerst.
1. Leaves acute.¹ Flowering cupule 1×1 mm., viscous, glabrous except for sparse hairs at the base. Low, at high altitude. *Fagus cliffortioides* Hook. f. New Zealand. 17. *N. cliffortioides* (Hook. f.) Oerst.

Subsect. 5. **Bipartitae** Steen., l.c. 146.

Cupule 2-valved, valves free to almost wholly connate, but in several cases the cupule is partly or wholly reduced. Lamellae entire. ♀ flowers 1 or 3, all 2-merous, flat. — TYPE: *N. brassi* Steen.

DISTRIBUTION: New Guinea and New Caledonia.

A. Series **Triflorae** Steen., l.c. 146.

Cupule with 3 ♀ flowers. ♂ flowers in triads. — TYPE: *N. brassi* Steen.

DISTRIBUTION: 4 species in New Guinea and 5 in New Caledonia.

B. Series **Uniflorae** Steen., l.c. 146.

Cupule with a solitary ♀ flower, sometimes very small or wholly suppressed. ♂ flowers in triads or solitary. — TYPE: *N. pullei* Steen.

DISTRIBUTION: 12 species in New Guinea.

¹This difference holds only for very typical specimens, but there are many atypical specimens. The differences given by Cockayne (cf. Poole, lit. ref. 38, p. 366, 373–374)

SPECIFIC DISTINCTION IN PAPUA

It is, in an unexplored group of species, often a puzzle how to delimit them if the material at hand is limited. In the case of Papuan *Nothofagus* the inadequacy of the material formed a formidable obstacle for an easy definition. For example, there is not a single collection among the fifty I had at my disposal which has both flowers and mature fruit. As is explained elsewhere in this paper, this is caused by the short duration of the period of anthesis and by the rather prolonged lapse of time between the flush and the fruiting stages. In many of the sheets female flowers are exceedingly scarce. Under such conditions one is tempted to describe too many species. There are marked additional vegetative characters for a number of species, but from the key based on vegetative characters only, it appears that there are some groups of species which agree closely in gross vegetative characters. On the other hand, some species, as, for example, 4. *N. brassi* and 16. *N. dura* are vegetatively exceedingly alike, but their cupular structures are widely different. It is possible that anatomical structures, e.g., the epidermal patterns, may yield microscopical distinctive characters, a task Miss Cookson has in view as a future project of research. Generally, sterile specimens are very difficult to place.

Though it is not unknown in the phytography of New Guinea that some genera have swarmed and show a rich speciation, as *Corybas*, *Tecomanthe*, *Trachymene*, *Xanthomyrtus*, *Drimys*, and *Sericolea*, I felt rather uneasy about specific delimitation of *Nothofagus*. It seemed to me that the distinctions that I made were finer and less marked than those found in the southern beeches. Mr. Brass wrote me Feb. 22, 1952, that, when he first looked over my conclusions and saw sixteen species described, including nine from the Archbold Expedition collections, he was a bit startled, but on marshalling his memories and going through his field notes, he thought I was probably right. In the necessarily narrow strip of country Mr. Brass covered on the Snow Mountains Expedition in 1938–1939, he recognized two or three species in different camp localities in the field. When species representation is like this in small areas, there is reason to think that *Nothofagus* has “swarmed” in New Guinea, and what might be the total number of species on that great island!

Mr. Brass wrote further “that the trees look pretty much alike in most cases, except for bark characters which may not be constant in a species that grows under varied habitat conditions and may change with the age of the trees, and except for their young-leaf colours, which are not always on display.”

Mr. Brass then stated his opinion, based in the field on the number of species he found different in each locality, and his numbers match exactly those of mine obtained independently on the basis of herbarium work.

are meagre. I believe these two species represent rather geographical vicarious subspecies of one specific population.

There are also other indications that my fears about distinguishing too many species are possibly not justified. I find to my satisfaction that of 7. *N. resinosa* I have two exactly matching collections, but one is from West New Guinea, the other from East New Guinea, places very wide apart. The same holds for 5. *N. pullei* which is known from Mt. Hellwig in West New Guinea, the only other collection being known from the Morobe District in East New Guinea. Also 12. *N. grandis* has been collected in both West and East New Guinea.

Another fact putting my conscience at ease is that Dr. Baumann-Bodenheim recognized in the field five species in New Caledonia with which I agreed at first sight.

As to the characters of the ♂ and ♀ flowers, I am of the opinion that the female flowers, the cupule, and the nuts provide the most reliable characteristics for specific delimitation. My drawback here has been that in a number of species only the flowering stage was represented and not the mature cupule and nut.

In those species with very much reduced cupular structures (species no. 5, 7, 8, 9, 10) there is no certainty whether and how mature cupules will develop. There is still a chance that these reduced cupules represent, by exception, what in silviculture is known as "Fehlschlagen," i.e. abnormalities falling outside the normal variability which may occur at the very beginning or at the end of the flowering season. For the present I have accepted them as normal characters.

Miss Cookson and Dr. H. E. Dadswell, both of Melbourne, have checked my species as far as possible with respect to the pollen structure and the wood anatomy, but the result is, unfortunately, not conclusive. In some cases these anatomical structures agree with gross morphological distinctions, but in other cases no distinction can be found, and in some cases no distinctions were found in what I regard certainly as good species on the basis of gross morphology. Both scientists agree that they themselves do not claim the characters obtained along their lines as finally decisive for specific delimitation.

As appears from the key the differential characters are not small; however, the question is whether they are good and will hold. Some new large-leaved collections have come to hand since the key was composed, and these could be easily placed, but the future will show whether this will also hold for the small-leaved ones.

With the material at hand I had the choice of describing a few very completely known distinct species and leaving the bulk unnamed, or endeavouring to work out all sheets to the best of my ability with the chance that a few species may have to be reduced later. I have preferred to accept the latter chance.

For future exploration it will be necessary, I think, to follow the Koorders method of numbering trees in the field (56) and making collections from these individual trees at different seasons of the year, in order to preserve for the herbarium a complete set of developmental stages from a year's cycle.

KEYS TO AND DESCRIPTIONS OF THE PAPUAN SPECIES

It is with some hesitation that the following key for determination of the Papuan species has been constructed. I found the characters of the ♀ sex the most valuable for this purpose, but I have as far as possible also made use of vegetative characters. My hesitation is mainly due to the fact that this study unfortunately had to be based on a rather meagre assemblage of material, though it comprises all which has been collected up to the present. The condition of the material is such that every specimen is in a certain stage of development, and as yet in hardly any species are all developmental stages of the cupule represented. Of single species only are mature cupules and nuts known. The number of ♂ flowers may represent a good additional character; however, in several species the male sex is unknown. Further, it is difficult to judge, from the herbarium, whether a cupule or female flower is full-grown, as the cupules, when dried, open in the immature stage. Therefore, the characters of the cupule and nuts are sometimes not wholly comparable. Some of the reductions in cupules might be ascribed to "Fehlschlage" and be abnormal. These are known to occur in *Fagus*, according to Celakovsky (42) and have occasionally been described in *Nothofagus*, e.g., one of the lateral ♀ flowers in *N. cliffortioides* 2-merous or one of the lateral ♀ flowers absent; in *N. cunninghami* Miss Langdon found a cupule with a central ♀ flower and two lateral ♂ flowers. On the basis of the present Papuan material no opinion can be offered in that respect. The scantiness of the material further excludes formulating an idea on the variability of the characters used for specific distinction. The reader is, therefore, obliged to verify his identification of future accessions by checking the result of his keying with the descriptions.

It would be well if there were a possibility of distinguishing all species by vegetative characters only. This seems to me to be out of the question. Several species show distinctive vegetative characters, but several others are very similar vegetatively. As far as such a key may be possible I have made one, following the present key.

TENTATIVE KEY FOR FERTILE MATERIAL

1. Cupule 3-flowered. Series TRIFLORAE.
 2. Leaves distinctly crenate, $5.5-7 \times 2.75-3.25$ cm. 2. *N. perryi*.
 2. Leaves entire.
 3. Cupule distinctly recurved. 1. *N. recurva*.
 3. Cupule erect or suberect.
 4. Midrib on the upper surface indicated by a groove but its proper tissue absent. Leaves rather thin-coriaceous, flattish, apex acutish. Nerves not sunken above. Reticulations distinct on the lower surface. Petiole medium. . . . 3. *N. starkenborghi*.
 4. Midrib distinct on the upper surface, sulcate, with an elevated ridge at least in the lower half of the blade. Leaves distinctly convex, hard-coriaceous, apex rounded. Nerves shallowly sunken above. Reticulations absent on either side. Petiole thick. 4. *N. brassi*.

1. Cupule 1-flowered. Series UNIFLORAE.

5. Twigs of the flush and preceding growth period distinctly¹ densely reddish-brown hairy. Stipules persistent. 5. *N. pullei*.

5. Twigs glabrous¹ or nearly so.

6. Leaves crenate, at least towards the apex of the leaf, flat, ovate-oblong, acutish, $2.75-4 \times 1.25-2$ cm. 6. *N. crenata*.

6. Leaf margin entire (or rarely very obscurely subcrenate in spp. 7 and 8 which possess a waxy leaf undersurface and rounded or obtusish leaf apex).

7. Leaves of flowering twigs distinctly covered with a grey or yellowish waxy film, flat, chartaceous.

8. ♀ flowers without cupule. Habit a bit coarser than that of the following species. 7. *N. resinosa*.

8. Fruit with a 1-lamellar, oblong cupule splitting to the base. Habit more slender than in the preceding sp.

. 8. *N. pseudoresinosa*.

7. Undersurface of leaves of flowering twigs without such a cover.

9. Leaves obovate, margin hardly recurved. ♂ flowers in peduncled triads, truncate-campanulate, with a distinctly constricted base. Cupule in flower reduced to 2 elamellar appendages, distinctly stalked. 9. *N. carri*.

9. Leaves ovate-oblong or elliptic. Cupule absent or at least with 2 or 3 lamellae.

10. ♀ flower ovate or ovate-oblong.

11. Cupule absent, its perianth limb specially produced towards the apex as rather patent appendages. Lateral sides of the ♀ flower with a central prominent rib at the tip of which is a small, sometimes glandular appendage.

. 10. *N. cornuta*.

11. Cupule distinct, with ca. 3 lamellae, narrow, $6-7 \times 2-2.5$ mm., in flower shorter than the ♀ flower, in fruit about as long as the nut.

. 11. *N. bernhardi*.

10. ♀ flower and nut about as long as broad.

12. Cupule ca. $12-15 \times 7-12$ mm., split halfway, with 3 or 4 lamellae. Nut rhomboidal, ca. 10 mm. through. Leaves large, ca. $3.5-7.5 \times 2-4.5$ cm. 12. *N. grandis*.

12. Cupule at most 10 by 5 mm., split somewhat deeper. Nut roundish, 4-5 mm. through. Leaves smaller, up to $2-4.5 \times 1.5-2.5$ cm.

13. Maturing ♀ flowers 3-5 mm. pedicelled, pedicels very distinct, recurved. Leaves small, ca. 2.5×1.5 cm., elliptic. ♂ flowers in 4-5 mm. peduncled triads.

. 13. *N. decipiens*.

¹The waxy film on the young parts in some species is sometimes covered by dark-coloured, patent sporophores of Fungi apparently belonging to the sooty moulds. In 1949 I sent a sample to Mr. Mason of the Imperial Mycological Institute at Kew asking detailed information, but there has been no answer as yet.

- 13. ♀ flowers sessile or at most 1.5 mm. pedicelled, erect. ♂ flowers in sessile or subsessile triads.
- 14. Style long, persistent, hence nutlets beaked. 14. *N. rubra*.
- 14. Style short or not persistent, nutlets not beaked.
- 15. Leaves elliptic, less than twice as long as broad, coriaceous. 15. *N. eymae*.
- 15. Leaves ovate-oblong, 2–2.5 times as long as broad, hard-coriaceous, distinctly concave. . . 16. *N. dura*.

TENTATIVE KEY BASED ON VEGETATIVE CHARACTERS

- 1. Leaves crenate in the upper half, ovate-oblong, acutish.
 - 2. Leaves firmly coriaceous, 6–7 × 2.5–3.5 cm. Prominent ridge in the midrib on the upper surface indistinct in the upper half. Petiole strong, ca. 0.75 cm. 2. *perryi*.
 - 2. Leaves thinly coriaceous, 3–4.5 × 1.5–2 cm. Prominent ridge extending to the leaf apex. Petiole thin, 0.25–0.5 cm. 6. *crenata*.
- 1. Leaf margin entire or almost so.
 - 3. Twigs distinctly hairy (stipules long-persistent). 5. *pullei*.
 - 3. Twigs glabrous.
 - 4. Undersurface of young but full-grown leaves distinctly covered with a grey or yellowish waxy film, flat. Margin very faintly crenate.
 - 5. Leaf texture thickish. 7. *resinosa*.
 - 5. Leaf texture thin. 8. *pseudoresinosa*.
 - 4. No such waxy film. Leaves flat or convex.
 - 6. Tissue of midrib on upper surface not visible within the groove, a fortiori without a prominent ridge. 3. *starkenborghi*.
 - 6. Tissue of midrib at least visible up to half its length and provided with a prominent ridge.
 - 7. Leaves thick-coriaceous, ovate-oblong, acutish, convex. Lateral nerves rather distinct. 1. *recurva*, 2. *brassi*, ?14. *rubra*, and 16. *dura*.
 - 7. Leaves thin to thick-coriaceous, broad-elliptic to obovate (if ovate-oblong then not convex), flat or at least not distinctly convex though margin often recurved.
 - 8. Leaves generally large, 5–10 × 2.5–5.5 cm. 12. *grandis*.
 - 8. Leaves smaller, up to 3–4 × 2–2.5 cm.
 - 9. Leaves generally obovate. 9. *carri*.
 - 9. Leaves elliptic or broad-elliptic. 1a. *recurva* var. *microphylla*, 10. *cornuta*, 11. *bernhardi*, 13. *decipiens*, 14. *rubra*, and 15. *eymae*.

1. *Nothofagus recurva* Steen. in Blumea 7: 146. 1952. — FIG. 4.

Monoecious, glabrous shrub or small tree 2–10 m. Twigs rather strong. Perules roundish, not much elongating. Leaves oblong to ovate-oblong, or



FIGURE 4. *Nothofagus recurva* Steen. a. twig with cupule, apical flush with ♂ flowers, b. stipule from inside, c. triad of ♂ flowers, c'. insertion of stamens in bud, d. two cupules, styles of ♀ flowers exserted, e. two mature cupules, f. two nuts. (After *Kostermans* 2384; a. nat. size, b-f. $\times 4$.)

elliptic, coriaceous, margin entire not strongly recurved, $4-7 \times 2-3$ cm., older ones up to 8×3.5 cm.; nerves 7-9 pairs, visible on the upper surface, very prominent below; reticulations indistinct above, slightly prominent beneath; glands mostly 0.5-0.75 mm. spaced. Petiole strong, 4-6 mm. Stipules caducous, large, oblong, $7-10 \times 3$ mm., thin except the concave insertion, attached at one third of their length. ♂ inflorescences on the basal part of bare short-shoots, in shortly peduncled or sessile triads. Perianth tubular, many-veined, minutely puberulous, 7-9 mm. long. Stamens ca. 15, filaments with scattered, patent hairs; anthers 5-7 mm. ♀ inflorescence 5-7 mm. stalked, 3-flowered, recurved, peduncle stout, thickened towards the apex; only the styles protruding above the roundish cupule 4-5 mm. in diam. ♀ flower roundish, including the thick wings more or less rhomboid; style 1 mm., distinct. Mature cupule ca. 10 mm. stalked on a stout, recurved peduncle, usually one found above the ♂ flowers, $7-10 \times 5-9$ mm.; lamellae 3, besides some indistinct apical ones. Nut (ripe?) broad-elliptic to ovate or rhomboid in outline, acute, 6×4 mm.

NORTHWEST NEW GUINEA: Mt. Arfak, Angi Gita Lake, *Kostermans* 2384 (BO, TYPE; L), 9-22 Oct. 1948, tree 10 m., flowers white; ibidem, 2000 m., *Kostermans* 2321 (BO, L), shrub 2 m., flowers white.

Apparently closely allied to 2. *N. perryi* but differs in the entire leaves and recurved cupular stalk. Both species are the largest-leaved among the Papuan representatives. The two specimens cited are exactly identical.

1a. *Nothofagus recurva* var. *microphylla* (Steen.) comb. nov. — FIG. 5.

Nothofagus pseudoresinosa var. *microphylla* Steen. in *Blumea* 7: 147. 1952.

Treelet, 6 m. Leaves elliptic-oblong, $2.5-4 \times 1.5-2$ cm., less coarse than in the species, side-nerves less prominent below.

NORTHWEST NEW GUINEA: Mt. Arfak, summit ridge of Mt. Kubré, 2000-2300 m., *Kanehira & Hatusima* 14052 (label on branch reads 14056), (A, TYPE; BO), April 9, 1940, treelet 6 m., flowers white, gregarious in burnt open forest especially in the vicinity of Iray, near Lake Angi Gita.

This is apparently a microphyllous form of exposed ridges. Though the leaves are very different in habit from those on the type of the species there are no additional differences and it may turn out to represent a phenotypic form of it. The ♂ triad is here 1-3 mm. peduncled, the ♂ perianth only 5 mm. long; according to Dr. Hatusima it has the following additional characters: tree 10-15 m., less than 30 cm. diam.; stamens 15-20; anthers 3.5-4 mm.; nuts narrowly winged, 6×3 mm.

It certainly resembles 13. *N. decipiens*, but has 3 ♀ flowers in each cupule, a thicker cupule, and short-peduncled ♂ flowers.

By a typing error this has earlier been referred to as a variety of *N. pseudoresinosa*.



FIGURE 5. *Nothofagus recurva* var. *microphylla* (Steen.) Steen. a. flowering twig, b. insertion of leaf with stipules, c. ♂ flower, d. ♀ inflorescence, left, one valve of cupule removed, right, from outside, e. ?mature cupule. (After Kanehira & Hatusima 14056; a. nat. size, b–e. enlarged.)

2. *Nothofagus perryi* Steen. in Blumea 7: 146. 1952. — FIG. 3, 6.

Glabrous tree. Ultimate twigs slightly zigzag, subapplanate. Perules roundish, 3 mm. long, elongating. Leaves ovate-oblong, coriaceous, $5.5-7 \times 2.5-3.75$ cm.; margin distinctly crenate except in the basal part, edge cartilaginous; base broadly cuneate; apex acutish, tip subemarginate with a mucronulate midrib; midrib sulcate above with a distinct elevated ridge in the lower two thirds; nerves 6–8 pairs, rather straight, obliquely patent, distinctly prominent on the lower surface, indistinctly so on the upper surface, each ending in a crenation; reticulations distinct below, less distinct above; glands mostly 0.75–1 mm. spaced. Petiole 4–6 mm. Stipules unknown, apparently caducous. Flowers unknown. ♀ inflorescences apparently distinctly peduncled. Mature (?) cupule 3–6 mm. peduncled, erect, roundish in outline, split over two thirds of its length, the larger ones $7-9 \times 6-8$ mm., fully grown apparently 11×13 mm., 16 mm. peduncled, hardly split; lamellae 3. ?Ripe nut flattish on one side, thickened on the other, rather irregular by mutual pressure, roundish, (including the 0.33–1 mm. broad wing), base truncate, apex broadly rounded with 4–5 curved slightly prominent longitudinal veins on either side, 4–5 mm. diam.

EAST NEW GUINEA: Papua, Central Division, Ononge, vern. *sama* (Fuyuge language), East Mt. Tafa, near Nemodi, 2100 m., *L. J. Brass* 5057a (A, TYPE), July, (collected by *Father F. DuBuy*); ditto, 2350 m., *L. J. Brass* 5057 (not seen), sterile, Sept. 17, 1933, dominant tree of tall forests towards Nemodi, fine large rough-barked, usually buttressed tree with dense crown of shortly spreading branches, leaves grey below, minutely toothed.

TERRITORY OF NEW GUINEA: Chimbu, *J. Gilmore*, (LAE, L), fruct. Dec. 1952.

The large leaves and regular nerves give a *Fagus*-like appearance to this species. The specimens are said to be supplementary to *Brass* 5057, which number I have not encountered among the loans. For the affinity cf. sub 1. *N. recurva*.

The fruits and twigs I hope belong together; they were detached. Vegetatively, the Gilmore collection matches the type exactly; it has one attached cupule which is much larger than the loose ones of the type, with four lamellae, and a very long peduncle (see above and compare *fig. 2e*). The species is named in honour of Miss L. M. Perry in appreciation for her help in securing the material for this paper and out of respect for her valuable contributions towards the flora of New Guinea.

3. *Nothofagus starkenborghi* Steen. in Blumea 7: 146. 1952. — FIG. 7.

Apparently monoecious tree up to over 30 m. tall, over 1 m. diam. Twigs minutely puberulous, glabrescent. Perule minute. Leaves oblong, subcoriaceous, $3-5.5 \times 1.25-2.25$ cm., generally ca. $2\frac{1}{2}$ times as long as broad, flat, tip emarginate, base broad-cuneate, margin cartilaginous, feebly recurved; midrib sulcate on the upper surface, without an elevated ridge, strongly prominent beneath; nerves ca. 6–8 pairs, indistinct on both

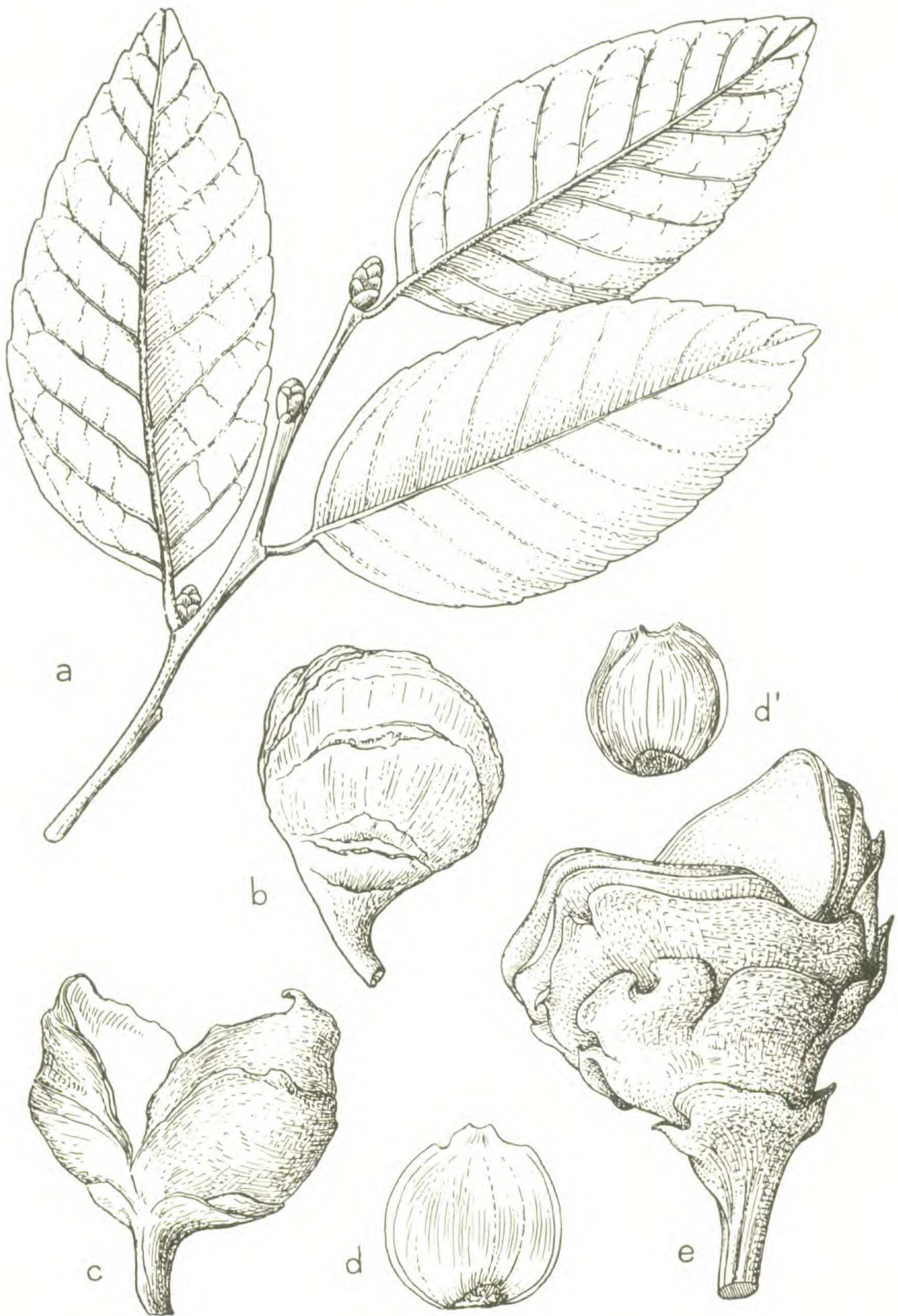


FIGURE 6. *Nothofagus perryi* Steen. a. twig, b-c. cupules, d-d'. two nuts, e. cupule. (After Brass 5057a; a. nat. size, b-d. $\times 4$; e. after Gilmore s. n., $\times 4$.)

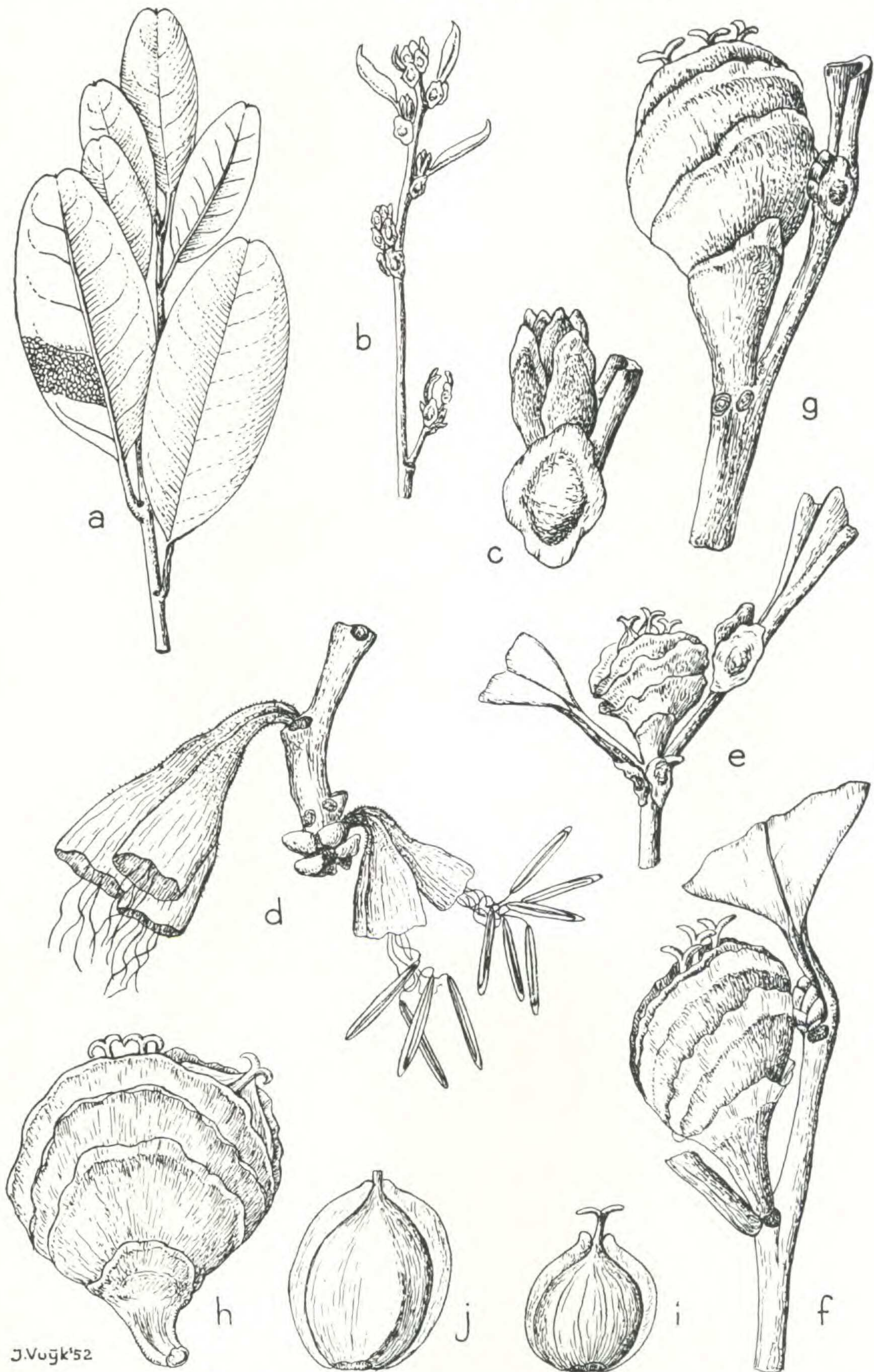


FIGURE 7. *Nothofagus starkenborghi* Steen. a. twig, b. flush, c. stipule with perule, d. ♂ flowers, e. young cupule, f-h. older cupules, i. ♀ flower, j. immature nut. (a-d., g, j. after Brass 11369, b, c. after Brass 11202, e, f, h, i. after Brass 11563; a, b. nat. size, c. $\times 5$, d-j. $\times 4$.)

sides; reticulations indistinct on the upper surface, somewhat prominent on the lower surface; glands on the lower surface ca. 0.5–1 mm. spaced. Petioles 4.5–7 mm., terete, upper surface sulcate with an elevated ridge. Stipules peltate, ovate, not very soon caducous, 2.5–4 × 1–2.5 mm. ♂ flowers (all detached) in recurved triads; pedicels nearly free from the base or over 2 mm. connate in a short peduncle; constricted basal portion of the perianth angled, ca. 2 mm. long, minutely hairy; perianth above the constriction campanulate-tubular, truncate, 2–4 mm. high, or more tubular 4–5 mm. high. Stamens ca. 12; staminal column reaching halfway the perianth-tube, filaments minutely hairy; anthers ca. 3 mm., nearly 0.75 mm. broad when open, apex and base minutely papillose-hairy, connective thickened-apiculate. ♀ inflorescence erect. Cupule ca. 3–4 mm. stalked, rounded, 7–9 mm. diameter; lamellae 2 or 3. ♀ flower broad-elliptic or roundish, ca. 6 × 4 mm., rather broadly winged, wings surrounding the basal part of the style; style 0.5–1.25 mm.

WEST NEW GUINEA: 18 km. NE of Lake Habbema, Camp at Bele River, 2200–2400 m., *L. J. Brass 11369* (L, TYPE; A, BO), November 1938, dominant tree on lower slopes of valley, up to over 30 × 1 m., trunk often spur-buttressed, bark pale grey-brown, lenticellate, shedding in hard thin sheets or larger scales, young leaves red, loose ♂ flowers belong to this tree (immature ♀); *ibid.*, 2250 m., *Brass & Versteegh 11107*, (A, L), dominant in primary forest, on slope of ridge, crown not wide-spreading, young leaves reddish brown, tree 22 m. × 53 cm., bark 1 cm. thick, gray scaly, outer wood rose, inner brown, young fruit green, ♀; *ibid.*, *Brass 11563* (A, L), ♀; *ibid.*, *Brass 11202* (A, L), very abundant and dominant at 2250 m. in gorge below camp, material from small tree 20 m. × 30 cm., yellow-grey close bark peeling horizontally in thin small flakes, ♀.

The material is singularly homogeneous, all specimens being, unfortunately, in approximately the same stage of development. The longish flat leaves are typical. Its closest ally is apparently 4. *N. brassi*.

The name of this tree is respectfully dedicated to His Excellency, Jhr. Mr. A. W. C. Tjarda van Starkenborgh Stachouwer, the last Governor General of the Netherlands Indies, 1936–1945, who was also one of the noblest of the Dutch administrators and regents in the Service, and to Mrs. Tjarda, whose brave, unselfish, and exemplary behaviour during the Japanese occupation was a beacon of faith to the P. O. W.'s and internees in their misery in the Japanese camps. Under his term of office several important expeditions were sent to New Guinea for botanical exploration of the island.

4. *Nothofagus brassi* Steen. in *Blumea* 7: 146. 1952. — FIG. 8–9.

Nothofagus sp. Langdon in *Bot. Gazette* 108: 358, *fig. 14–17*. 1947.

Monoecious tree up to 40 m. by over 1 m. diam., twigs coarse, faintly zigzag, internodes slightly flattened. Perules ovate, ca. 4 mm. Leaves elliptic-oblong, 3.5–5.5 × 1.5–2.25 cm., entire hard-coriaceous, the margin strongly recurved, upper surface glossy, apex somewhat acutish; midrib

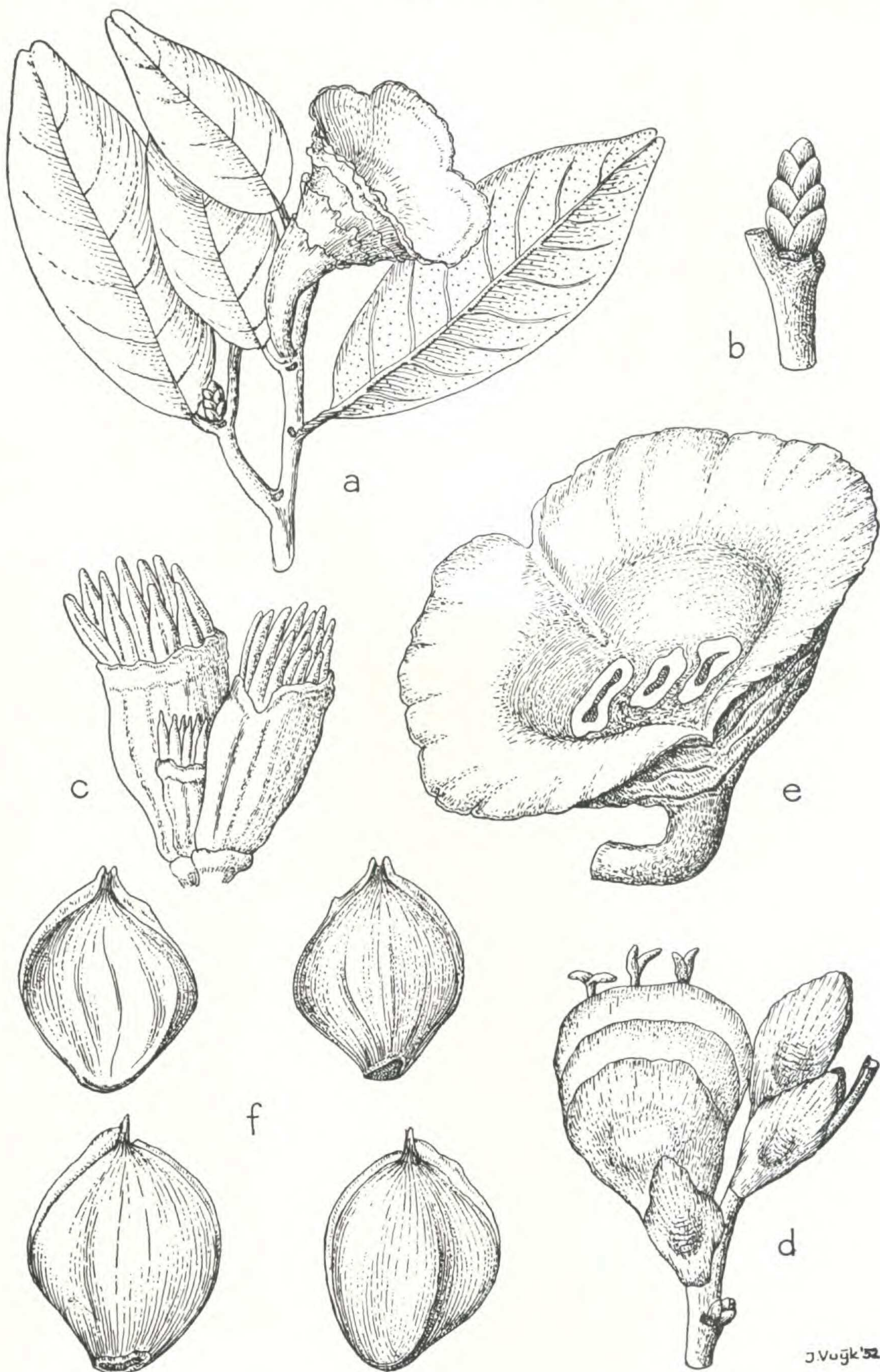
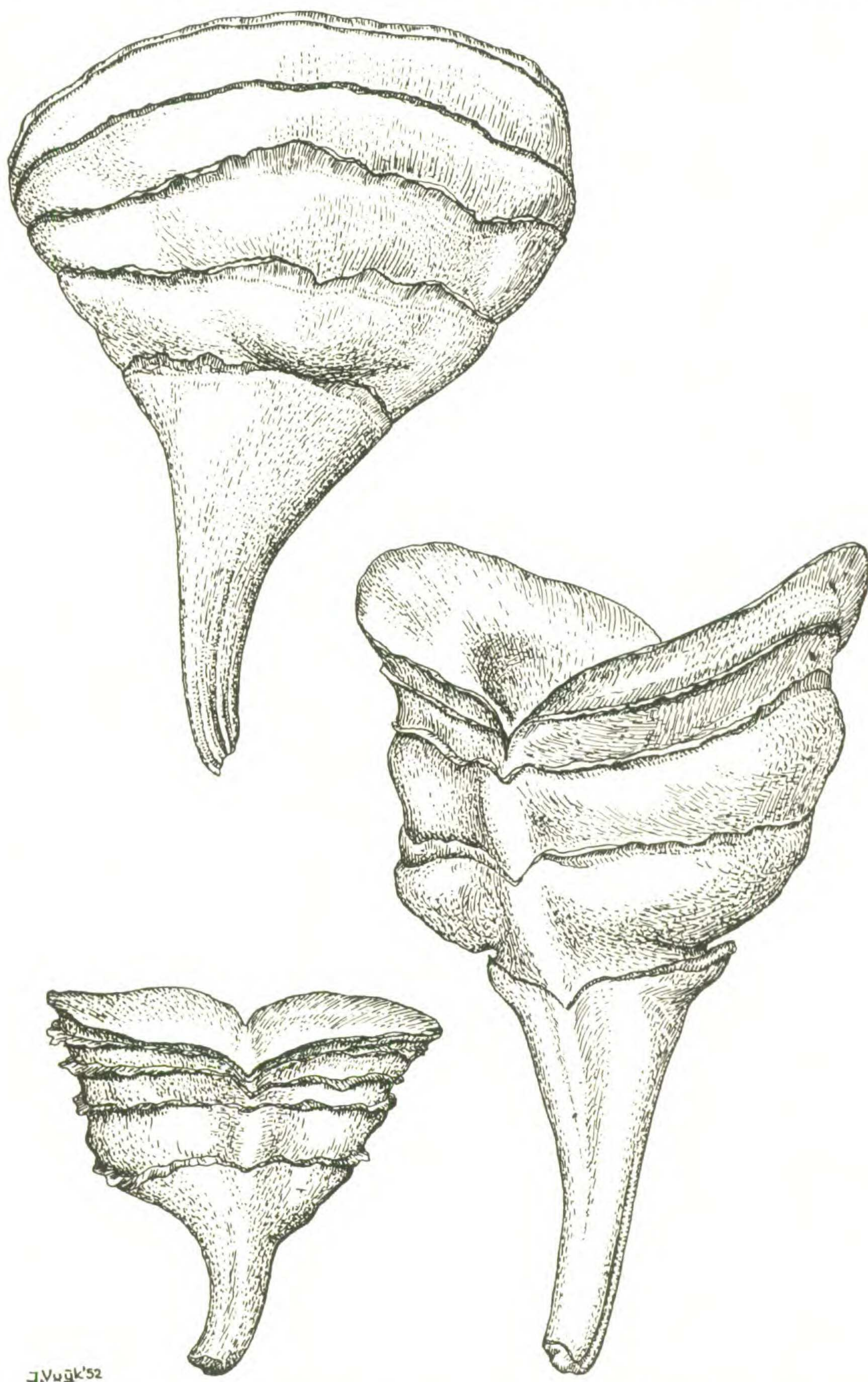


FIGURE 8. *Nothofagus brassi* Steen. a. fruiting twig, b. perule, c. triad of ♂ flowers, d. flowering cupule, e. mature cupule, f. nuts. (After Brass 11115; a. nat. size, b-f. $\times 4$.)



J. V. G. '52

FIGURE 9. *Nothofagus brassi* Steen. Three cupules seen from various angles, $\times 4$. (After Brass 11115.)

strongly prominent underneath, terete, on the upper surface sulcate with a prominent ridge; primary nerves 7 or 8 pairs, slightly sunken on the upper surface, distinct but faintly prominent underneath; reticulations on the upper surface absent, indistinct underneath; glands distinct on the lower surface, 0.5–0.75 mm. spaced. Petiole stout, ca. 0.5 cm. Stipules peltate, acute-oblong, $5-6 \times 2.5$ mm., early caducous, attached in the lower part. ♂ flowers (not seen by me, hardly any observed by Miss Langdon, l.c.) in triads, orange (acc. to Brass), rather tubular, $\pm$ sessile, limb truncate 3-toothed; anthers ca. 15. ♀ inflorescence erect, peduncled; flowers 3 (1 or 2 laterals sometimes abortive and sterile), ovate, wings surrounding the style-base; style 1–2.5 mm. Cupule about as large as the ♀ flowers, roundish, split halfway down, when young ca. 1 cm. peduncled, and 1 cm. broad, later when ripe ca. 1.25 cm. peduncled, ca. 1.5 cm. through, distinctly 4–5-lamellate, thick woody. Nuts very different in shape by mutual pressure, often partly abortive, ovate to broad-ovate, or suborbicular, distinctly winged towards the apex, averaging 6×6 to 9×6 mm., the largest ones ovate, 10×6 mm. inclusive of apical wings.

WEST NEW GUINEA: Bele River camp 18 km. NE of Lake Habbema, ca. 2300 m., *Brass & Versteegh 11115*, (L, TYPE; A, BO), November 1938, dominant tree in forests of upper slopes, up to 40 m. by over 1 m., ♂ flowers orange, ♀ flowers red, fruit brown-green, bark 1 cm. thick, rough, brown, fissured, scaly, outer wood brown, inner wood red-brown; *ibid.*, 9 km. NE of Lake Habbema, 2680 m., *Brass & Versteegh 11103* (A, BO, L), October 1938, dominant tree of rain-forest on slope of ridge, tree 27 m. by 39 cm., crown not wide-spreading, bark 8 mm., rough, scaly, fissured, outer wood brown, inner wood red-brown, fruit brown.

The two collections cited agree markedly. This species occurs apparently in the same area as 3. *N. starkenborghi*, but at higher altitude. It can readily be distinguished from the latter species by its hard, more convex leaves showing a distinct ridge on the sulcate midrib. Possibly there are additional characters of the fruit which are not yet known in *N. starkenborghi*.

This species is named after Mr. L. J. Brass in honour of his unrivaled collections of New Guinean plants in general and of *Nothofagus* in particular. In returning from the Third Archbold Expedition he had recognized the identity of the Papuan trees.

5. *Nothofagus pullei* Steen. in *Blumea* 7: 146. 1952. — FIG. 10.

Monoecious. Shrub, widely branched treelet, 2–4 m. high, or tall tree; bole up to 30 cm. diam. Twigs terete, densely brown-pubescent, hairs persistent. Flush light green, the very young leaves thickly covered with orbicular, thickish scales. Perules roundish, 1–1.5 mm. diam. Leaves hard-coriaceous, elliptic-oblong, $1.75-3 \times 1-1.75$ cm., both ends rounded, margin entire, recurved, cartilaginous; upper surface smooth, subglossy, eglandular, midrib sulcate, with a distinct elevated ridge at least in the lower half; undersurface sparsely hairy on the thick, very prominent midrib; primary nerves ca. 6 pairs, distinct; reticulations dense, distinct on the

lower surface, not so above; glands on the undersurface 0.33–0.5 mm. spaced. Petiole 1–3 mm. Stipules ca. $4-5 \times 2$ mm., persistent, oblong, attached below the middle. ♂ flowers solitary, erect; perianth subcampanulate, ca. 6–7 mm. long. Stamens ca. 15; filaments slightly hairy; anthers ca. 4 mm. long, glandular on the back. ♀ inflorescence sessile.

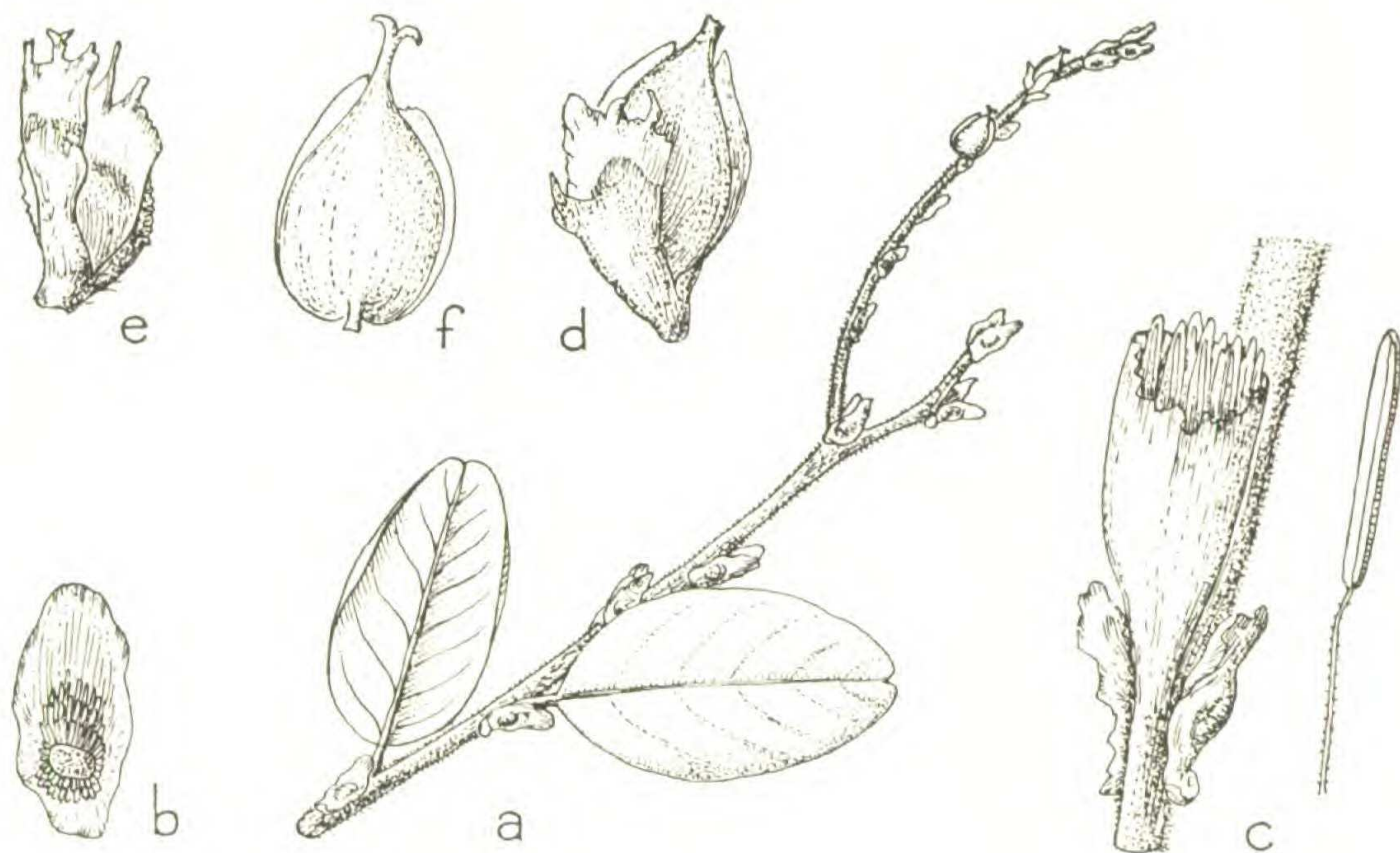


FIGURE 10. *Nothofagus pullei* Steen. a. twig with flowering flush, b. stipule (underside), c. ♂ flower and stamen, d. cupule with ♀ flower, e. same cupule with flower removed, f. ♀ flower separately. (After Pulle 909; a. nat. size, b–f. $\times 4$.)

Immature cupule with unequal valves, both of which are narrower and shorter than the ovary, one valve straight, roundish, entire or toothed, the other curved and with glandular-tipped lobes or teeth, ca. 3.5×2.5 mm., both with one lamella. ♀ flower ovate to $\pm$ elliptic, with distinct perianth wing, ca. 5×2.5 mm.; style distinct, thick, ca. 1.5 mm.; stigmas thick, 1 mm. Mature cupule and nut unknown.

WEST NEW GUINEA: Mt. Hellwig, 2600 m., A. A. Pulle 909 (BO, TYPE; L, U), January 4, 1913, scrub on ridge, shrub or treelet, 2–4 m. high.

NORTHEAST NEW GUINEA: Morobe Distr., Masalk River, at base of Mt. Sarawaket, Clemens 7510 (A, L), mountain forest, tall tree, 30 cm. diam., stamens vivid blood-red, filaments white.

This species has the reduced cupule (in flower) in common with 7. *N. resinosa*, 9. *N. carri*, and 10. *N. cornuta*, and it seems to be most closely allied to the last species, of which some specimens show a faint hairiness on the youngest parts, rather long-persistent stipules, and a similar nervature. It differs from *N. cornuta* in its conspicuous indumentum, terete twigs, and a different shape of the cupular valves.

The East New Guinean specimens agree in flower with those of West New Guinea, but the leaves are somewhat rounder, $1.5-2 \times 1.25-1.75$ cm.; they possess many ♂ flowers and show no ♀ ones, whereas the West New Guinean specimens had more ♀ than ♂ flowers.

This species has been named in honour of Prof. Dr. A. A. Pulle, who was the first to collect a *Nothofagus* in New Guinea.

6. *Nothofagus crenata* Steen. in Blumea 7: 147. 1952. — FIG. 3, 11.

Glabrous tree, up to 40 by over 1 m. Perules roundish, ca. 1 mm. Leaves flat, thinly coriaceous, ovate-oblong, symmetric or suboblique,



FIGURE 11. *Nothofagus crenata* Steen. a. ♀ flowering twig, b-c. cupules with ♀ flower, d. ♀ flower. (After Brass 11335; a. nat. size, b-d. $\times 4$.)

$2.5-5 \times 1.25-2$ cm.; base cuneate; apex attenuate; margin towards the apex shallowly crenate-sinuate, with a caducous, minute, sausage-shaped appendage mostly inserted at the nerve-ends; primary nerves 5-6 pairs, faint; veins on the upper surface somewhat prominent, on both surfaces tessellate-reticulate; glands 0.5-1 mm. apart. Petiole 4-5 mm. Stipules early caducous, ovate, 5×2 mm. ♂ flowers (only loose stamens found, not with certainty belonging to the species); filaments sparsely pubescent; anthers 5 mm. ♀ inflorescences (after anthesis) in all the leaf-axils of the young shoots, erect, ca. 5 mm. stalked, stalk thickened towards the apex. Immature cupule split to the base, glabrous, finally as large as the flower, about orbicular in outline, $4.5-6 \times 5-6$ mm.; lamellae ca. 3 or 4, the lowermost loose. ♀ flower solitary, $\pm$ orbicular, distinctly winged, apical

teeth reaching the style-base, ca. 5×4 mm.; style 0.5 mm.; stigmas 0.5 mm. Mature cupule and nut unknown.

CENTRAL WEST NEW GUINEA: Bele River, 18 km. NE of Habbema Lake, 2400 m., *Brass 11335* (L, TYPE; A, BO), fl. November 1938, vern. *n'gi*, common in forests, large tree, up to 40 by over 1 m., bark gray-brown, thinly scaly.

Not obviously allied to any other species, as the only other one with distinctly crenate leaves, viz., 2. *N. perryi*, possesses 3 ♀ flowers in the cupule. It is uncertain whether the ♂ flowers belong to the specimen; if so, the ♂ flowers are apparently inserted close to the axils of the perular bracts.

7. *Nothofagus resinosa* Steen. in *Blumea* 7: 147. 1952. — FIG. 3, 12.

Monoecious. Glabrous tree up to over 40 m. high, more than 1 m. diam.; twigs brownish. Perules roundish, 2–3 mm. Lower surface of the leaves, stipules and flush conspicuously covered by a pale, slightly yellowish, waxy exudation. Leaves elliptic, coriaceous, rounded at both ends, flat, margin cartilaginous and practically entire, blade $\pm$ symmetric to $\pm$ unequal-sided, $4.5\text{--}7 \times 2\text{--}4$ cm., in fruit up to 10×5 cm.; upper surface smooth; primary nerves ca. 9 pairs, feebly prominent on the under surface, as are the inconspicuous reticulations; glands 0.5–1 mm. apart. Petiole 5–8 mm. Stipules elliptic, caducous, 4–6 mm. long. ♂ flowers solitary, erect, on naked short twigs and axillary, subsessile to 1 mm. pedicelled, minutely puberulous, trumpet-shaped, 6–7 mm. long. Stamens ca. 13, filaments sparsely hairy; anthers 3–4 mm. ♀ inflorescence consisting of an ecupular, solitary, erect, sessile, ovate-oblong, minutely puberulous flower, ca. $6\text{--}7 \times 3.5\text{--}4$ mm.; wings narrow, reaching the style-base; style very short; stigmas 1.5 mm. Nut flat, broadly elliptic, $9\text{--}10 \times 6.5\text{--}7.5$ cm., wings shouldering the style base; conical apex 1 mm.; style persistent, 1 mm. Cupule a roundish, not hardened, flat basal appendage 2 mm. through.

CENTRAL WEST NEW GUINEA: 9 km. NE of Lake Habbema, 2680 m., *Brass & Versteegh 10479* (L, TYPE; A, BO), October 1938, dominant tree in rain-forest on ridge, up to 35–40 by more than 1 m., crown fairly wide-spreading, bark 7 mm. thick, rough fissured, outer wood brown, inner red-brown, ♂ flowers soft yellow.

NORTHEAST NEW GUINEA: Morobe Distr., Samanzing, 2100–2400 m., *Clemens 9457* (A), January 7, 1939, tall tree, meadow camp, mossy bush, sterile, perules just developing; Finschhafen Subdistrict, Joangen to Yunzaing, 1500 m., *Womersley N. G. F. 5134* (LAE, L), fruiting April 25, 1953.

DOUBTFUL SPECIMEN: West New Guinea, 9 km. NE of Habbema Lake, 2800 m., *Brass & Versteegh 10448* (A, L), October 1938, occasional tree of tall forest, 23 m. by 38 cm., crown not wide-spreading, bark 6 mm. thick, scaly, gray, outer wood white, inner brown.

This species shows in both specimens a comparatively strong exudation of a yellowish resin, especially on the flush, the perules, the undersurface of the leaves and the inner side of the stipules. It is this character to which

the specific name alludes. This resinous layer is often overgrown by a black fungus apparently belonging to the sooty moulds. The sporangio-phores are branched at their apex and give superficially a dark velutinous appearance. Whether this resin is conspicuous only in certain stages of development is not known; it is very typical. A doubtful sterile specimen

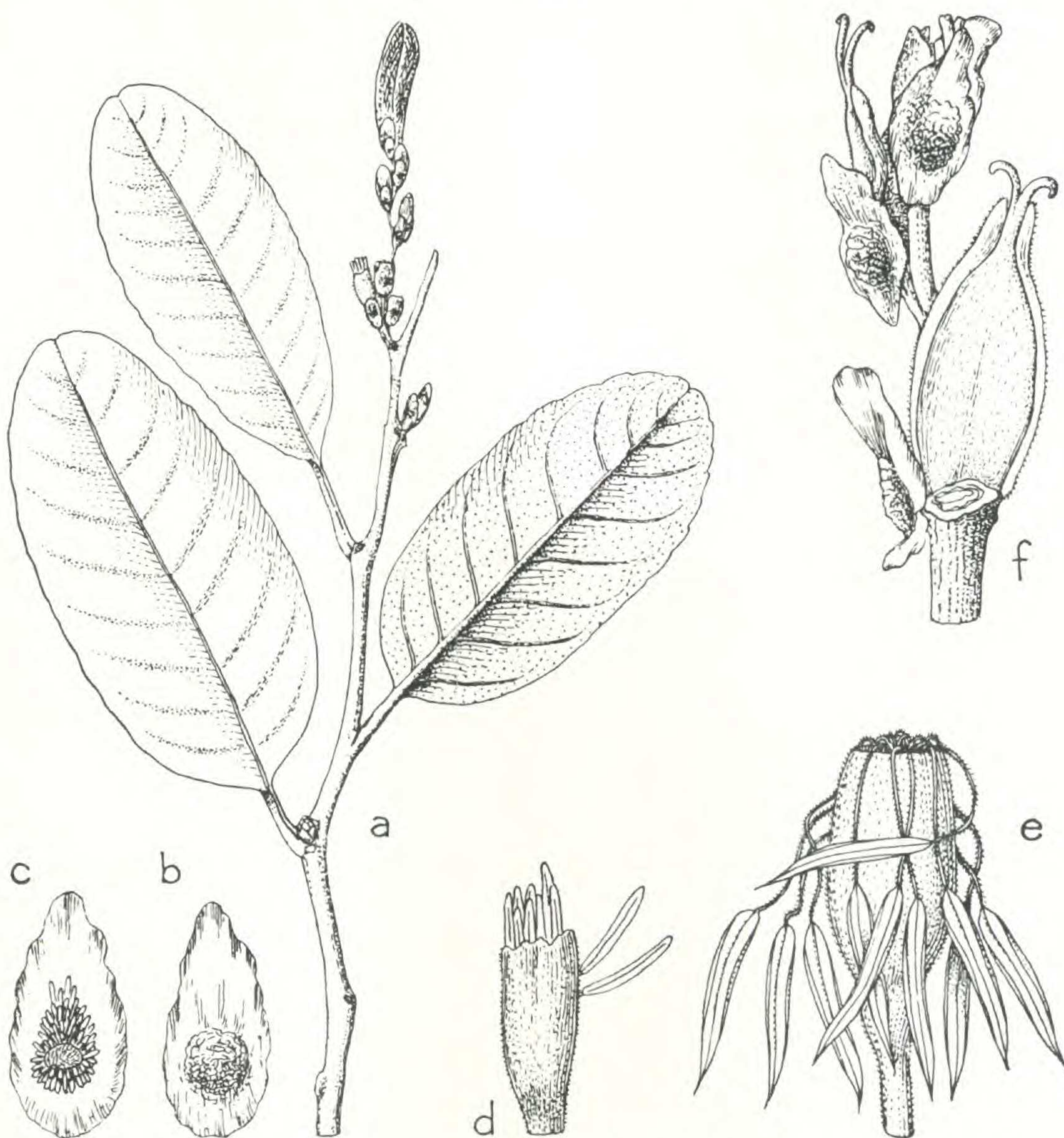


FIGURE 12. *Nothofagus resinosa* Steen. a. twig with flowering flush, b. stipule, outside, c. ditto, inner surface, d. immature ♂ flower, e. ♂ flower, f. flush with two ♀ flowers, lower one in front clear, one stipule removed. (After Brass 10479; a. nat. size, b-e. $\times 4$.)

which apparently belongs here does not show it distinctly; it is presumably taken from a young tree.

The only species with which to compare it is 8. *N. pseudoresinosa*. In the foliage it shows some resemblance to certain sheets of 12. *N. grandis*, but the ♀ flower is very different from the one in that species, and the ♂ flower is solitary.

The two flowering collections match exactly, though collected at a great distance.

The collection in fruit by Womersley is apparently conspecific, and the reduced cupule supporting the nuts is typical; it does not show, of course, the waxy flush, and the leaves are naturally somewhat larger than in the type.

8. *Nothofagus pseudoresinosa* Steen. in Blumea 7: 147. 1952. — FIG. 13.

Glabrous tree. Twigs comparatively thin. Perules round, 2 mm. Leaves densely placed, elliptic-oblong, flat, thinly coriaceous, $2.5-5 \times 1.25-2.5$

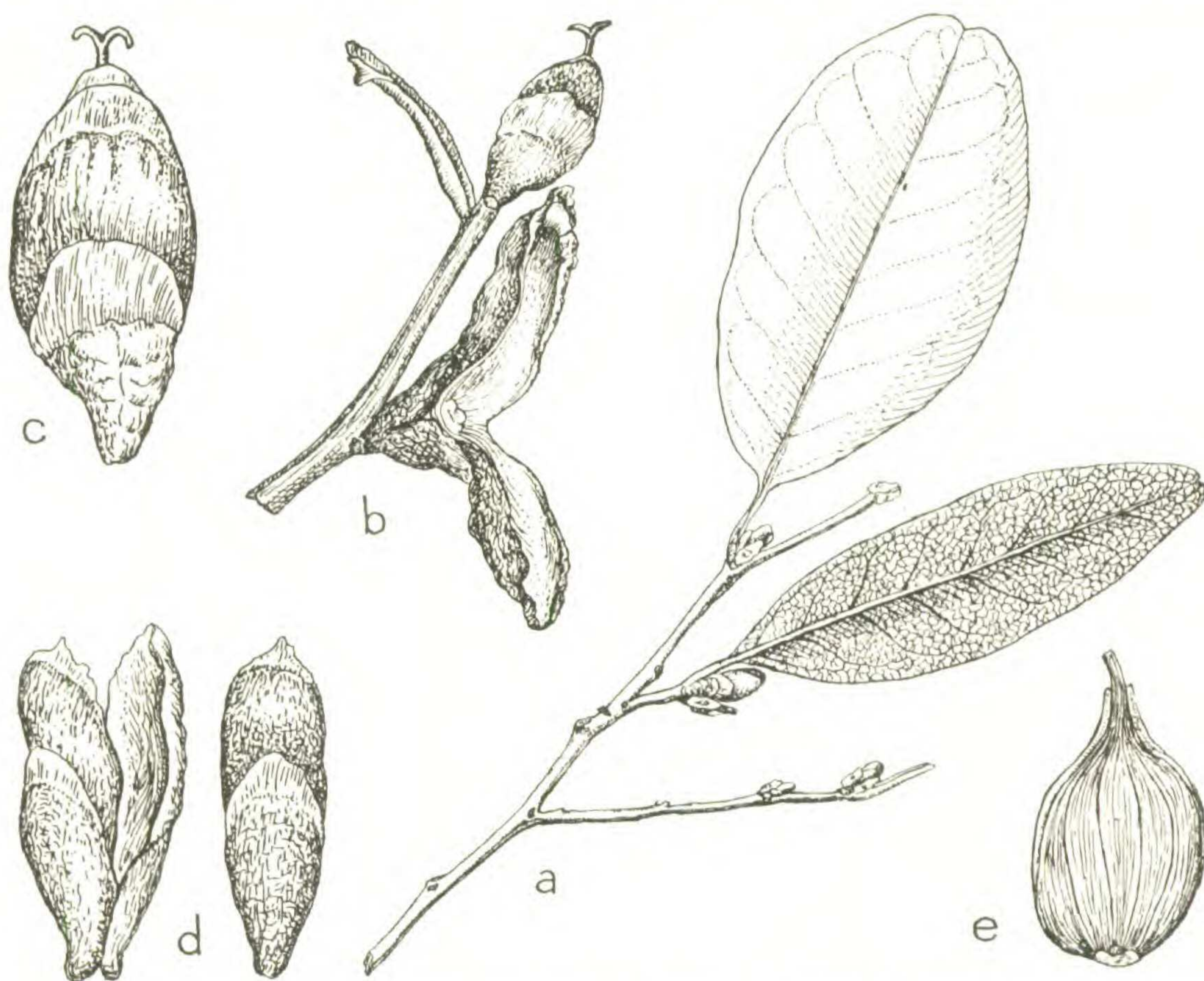


FIGURE 13. *Nothofagus pseudoresinosa* Steen. a. twig, b. ditto with flowering cupule and mature one, c. flowering cupule, d. older cupules, e. mature (?) nut. (After Clemens 5849; a. nat. size, b-e. $\times 4$.)

cm., base broadly cuneate, apex broadly cuneate to rounded; underside yellowish grey by a distinct resinous coat; midrib sulcate with an elevated ridge in the lower half, distinctly prominent beneath; nerves ca. 8 or 9 pairs, slightly more prominent than the reticulations; reticulations dense, prominent on both surfaces. Petiole more or less laterally compressed, 4–6 mm. long. Stipules early caducous, comparatively small, $3-4 \times 1.5$ mm. ♂ flowers unknown. Cupule sessile, 7–8 by 4–5 mm., split to the base, with one lamella halfway and another indicated higher up, obovate-oblong,

widely gaping when dry. ♀ flower roundish ovate, acuminate, $4-5 \times$ ca. 2.5–4.5 mm. Sides with 4 longitudinal nerves. Wing distinctly developed and produced above the insertion of the style; style distinct, ca. 1.5 mm.; stigmas 0.5 mm., feebly 2-lobed at the apex. Ripe nut unknown.

NORTHEAST NEW GUINEA: Morobe Distr., Mt. Sarawaket, 2400–2700 m., *M. S. Clemens* 5849 (A, TYPE), April 1937.

DOUBTFUL SPECIMEN: ibidem, 1800–2400 m., *M. S. Clemens* 7553 (A), November 9, 1937, big tree, 45 m., sterile specimen.

The type has only female flowers, as the tree was apparently beyond anthesis. The closest ally of this species is 7. *N. resinosa*, which it resembles very much vegetatively. The structure of the female flower is, however, constant in all flowers examined and differs greatly from that of *N. resinosa*, which is ecupular.

9. *Nothofagus carri* Steen. in *Blumea* 7: 147. 1952. — FIG. 3, 14.

Monoecious, glabrous tree, 20–33 m. tall. Twigs subglabrous. Leaves obovate, $\pm$ flat, coriaceous, rounded at both ends, $2-4.5 \times 1-2.5$ cm., margin entire, feebly recurved; nerves ca. 5–7 pairs, indistinctly prominent on both sides; reticulations dense and fine but hardly prominent; midrib with an elevated ridge only in the lower half; glands 0.5–1 mm. apart. Petiole 2.5–5 mm. Stipules early caducous, oval mostly oblique, $2-2.5 \times 1.25-1.75$ mm. ♂ flowers sessile in 1–3 mm. peduncled, patent triads on short efoliate twiglets, perianth hypanthium-like contracted at the base, campanulate or urceolate, 3.5–4 mm. long. Stamens ca. 10; filaments 8–10 mm., minutely papillose; anthers 2.5–3 mm. ♀ inflorescences erect, 1.5 mm. peduncled, very few. Immature cupule much shorter and narrower than the ovary, entire; valves unequal, oval to oblong, simple (i. e., without lamellae), 2–3 mm. long. ♀ flower solitary, flat, ovate, attenuate towards the apex, narrowly winged, 5×3 mm., wings reaching the style-base; style 1.5 mm. long. Mature cupule and nut unknown.

SOUTHEAST NEW GUINEA: below The Gap, 2100 m., *Carr* 15028 (L, TYPE), January 8, 1936, in forest, tree 30 m., flowers green suffused red, stamens red (only ♂ flowers found); ibidem, 1950 m., *Carr* 13766 (L), December 13, 1935, tree 21 m., flowers red (only ♂ flowers found); ibidem, *Carr* 15076 (L), January 13, 1936, tree 24 m., flowers red.

TERRITORY OF NEW GUINEA: Chimbu, *J. Cavanaugh* N. G. F. 3328 (LAE, L), February 1950, sterile, vern. *gripe*; ibidem, *J. Cavanaugh* N. G. F. 3330 (LAE, L).

The three numbers of Carr match exactly.

10. *Nothofagus cornuta* Steen in *Blumea* 7: 147. 1952. — FIG. 3, 15.

Subglabrous tree. Twigs distinctly angular. Perules oval ± 2 mm. diam. Leaves broadly elliptic or slightly ovate, $\pm$ flat; margin entire, not or only slightly recurved; base broadly cuneate or rounded, apex rounded 2.5–4



FIGURE 14. *Nothofagus carri* Steen. a. twig with flowering flush, b. detail of flush with one triad of ♂ flowers and one ♀ flower in a higher axil, c. ♀ flower from two sides, d. stamens in bud (perianth removed). (After Carr 15028; a. nat. size, b-c. $\times 4$.)

$\times 1.5$ – 2.25 cm.; midrib not sulcate above, consisting of a prominent ridge, distinctly prominent beneath; nerves ca. 6 pairs, slightly prominent above, faintly so below as are the reticulations, which are dense and prominent at both sides; underside of the immature leaf of the flush densely set with scales. Petiole 2–3 mm. Stipules rather long-persistent, $3\text{--}4 \times 1.5$ mm. ♂ flowers (two small detached ones found) apparently sessile, tube trumpet-shaped, 3.5–4 mm. long; anthers 2 mm. ♀ inflorescence sessile, without cupule. ♀ flower oblong, 4.5×2 mm., with obscure wings, the limb produced as two horn-like rather patent appendages; flat sides of the flower with a prominent midrib producing a glandular, short perianthal appendage below the limb; style 0.5 mm.; stigmas 0.75 mm. Nut unknown.

WEST NEW GUINEA: Wissel Lake region, base of Bubeiro and Enarotali, 1750 m., *Eyma* 5122 (L, TYPE; BO), August 1939; ibidem, 1750–1810 m., *Eyma* 4870-ter (BO), April 13, 1939, sterile; ibidem, *Eyma* s.n. (BO, L), sterile.

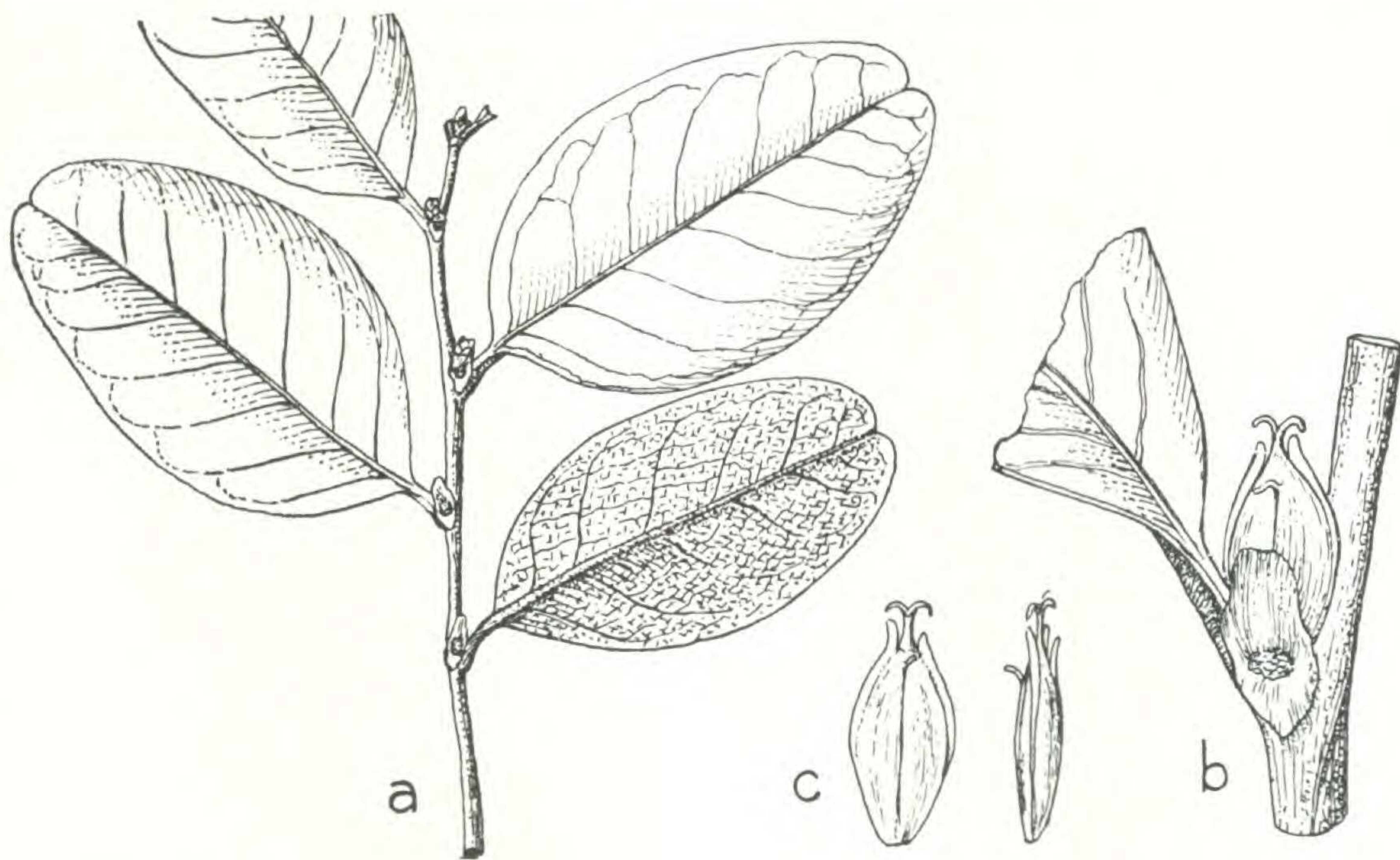


FIGURE 15. *Nothofagus cornuta* Steen. a. twig, b. ♂ flower partly hidden by stipule, c. ♀ flower. (After *Eyma* 5122; a. nat. size, b-c. $\times 4$.)

I have found only two ♀ flowers; their scarcity points to a stage beyond anthesis, and their peculiar cupular structure might be due to a "Fehl-schlag," though otherwise both flowers have a normal appearance. The few ♂ flowers were not attached to the twig; whether they stand in triads I do not know with certainty; I assume them to be inserted in that manner.

The species is apparently common in the Wissel Lake region. It is allied to 5. *N. pullei*, and shows in some of the flush a faint hairiness but differs in the distinctly angular glabrous twiglets, in the absence of a cupule, and the presence of minute perianthal appendages on the flat sides of the ovary.

In foliage it resembles 15. *N. eymae*, and some other small-leaved species.

11. *Nothofagus bernhardi* Steen. in *Blumea* 7: 147. 1952. — FIG. 16.

Gnarled, stiff, glabrous, monoecious, large tree, or a shrub 3–5 m. tall; flush red. Leaves oblong-elliptic, rounded at both ends, hard-coriaceous; margin entire, strongly recurved, thick; apex shallow-emarginate, 2.5–3.5 $\times$ 1.25–2 cm.; midrib sunken above with elevated ridge, strongly prominent and very sparsely minutely puberulous beneath; nerves ca. 5–7 pairs, hardly visible, not prominent; glands on the underside distinct, 0.5–1 mm. spaced. Petiole 2.5–5 mm. long, thick, semi-terete, margins elevated. Stipules obovate-oblong, inserted below the middle, early caducous, 7 $\times$ 3–3.5 mm. ♂ flowers red, numerous, mostly in the axils of perular bracts on the defoliate base of the flush, in triads, middle flower first in bloom; pedicels short, coalescent, 1–2 mm. long; perianth tubular, glandular, ca. 5 mm. long, limb shortly 3-lobed. Stamens ca. 10; filaments minutely

hairy, up to 2.5 cm. long; anthers linear, 3–3.5 mm. long, minutely puberulous, connective tip developed. ♀ inflorescences solitary, erect, very few in number above the ♂ ones. Flowering cupule smaller and narrower than the developing flower, flat, with free valves ca. 4 mm. long; lamellae 2 or 3, the inner ones initially hidden under the outer one. Unripe nut



FIGURE 16. *Nothofagus bernhardi* Steen. a. twig, b. part of flush enlarged with a triad of ♂ and 1 ♀ flower, c. ♀ flower, d. mature (?) cupule, opened, e. ditto, laterally, f–g. cupule with ?immature nut, h. ?immature nut. (a–c. after Brass 12453, d–h. after Brass 10243; a. nat. size, b–h. $\times 4$.)

ovate, neck elongate, perianth forming a distinct wing reaching up to the style, finely puberulous, 2 mm. stalked, the largest seen 8×4 mm.; style 2 mm. long; stigmas thick, flat, short. Infructescence (after Brass 10243) sessile, erect, cupule split to the base, gaping, much narrower than the nut, with 2 lamellae of which the upper is thin, the lower thicker than the upper one, minutely puberulous, $5-6 \times 1.5-2$ mm. Nut minutely puberulous, $4-6 \times 2.5-3$ mm.

WEST NEW GUINEA: 18 km. SW of Bernhard Camp, Idenburg River, 2150 m., *Brass* 12453 (L, TYPE; A, BO), February 1939, major component of low mossy forest scrub on exposed summit, gnarled stiff tree 2–5 m., leaves very stiff, convex, young ones reddish, tinging and characterizing the forest, anthers pink, ♂ and ♀ protandrous flowers; ibidem, 9 km. NE of Lake Habbema, 2800 m., *L. J. Brass* 10243 (A, L, BO), November 1938, characteristic tree of tall valley forests, fine large tree 30–40 m. by over 1 m., trunk shortly flanged or spur-buttressed at base (flying buttresses sometimes developed under very mossy conditions), bark rough, dark gray, irregularly scaly, wood hard, red, ♀ tree, in young fruit; ibid., *L. J. Brass* 10244 (A, L, BO), November 1938, sapling 20 m. by 20 cm., midrib of leaves red below.

The fruiting and flowering specimens differ a little according to the stage at which they were collected. As Mr. Brass found no ♂ flowers in the fruiting specimens he assumed the tree to be dioecious; however, in these specimens there are naked axils below the fruits on each twig which may have been occupied by the ephemeral ♂ flowers (as in *Brass* 12453). I have no hesitation in referring the fruiting specimens to the same species as the flowering ones.

The short pedicel of the peduncle of the flowering cupule disappears in the fruiting stage through the thickening of the woody base of the latter.

In very young ♀ flowers the lamellae of the cupule are packed, they telescope apart later.

12. *Nothofagus grandis* Steen. in *Blumea* 7: 147. 1952. — FIG. 17, 18, PL. I.

Tall tree. Twigs greyish, angular. Perules ca. 2 mm., obovate. Leaves entire, coriaceous, elliptic-oblong to broad-elliptic, $4.5\text{--}7 \times 2\text{--}4.5$ cm. (of saplings larger), flat, margin hardly recurved; midrib sulcate with an elevated ridge, prominent below; nerves ca. 7–8 pairs, somewhat prominent above but less so beneath; reticulations fine, slightly prominent on both sides; glands on the lower surface ca. 0.3–0.5 mm. spaced. Petiole 3–7 mm. Stipules early caducous, $5\text{--}6 \times 3\text{--}3.5$ mm., attached in the middle. ♂ flowers (coll. Schindler) in triads in the axils of perular bracts and a little higher; perianth club-shaped, tubular, 5–6 mm. mostly splitting spathaceously, rarely 5-lobed. Stamens 12–17; filaments hairy; anthers 3.5–4 mm., apiculate. ♀ inflorescences erect. Cupule roundish, with 2 lamellae. ♀ flowers (after Schindler) somewhat larger than the cupule, roundish, ca. 3 mm. long; style 1 mm. Ripe cupule woody, sessile, erect, split half-way, broad-obovate, apex nearly truncate, $12\text{--}13.5 \times 7.5\text{--}10$ mm. Nut distinctly rhomboid, narrowly winged, $7\text{--}10 \times 9.5\text{--}10$ mm.

EAST NEW GUINEA: Territory of New Guinea: Aiyura, rain-forest, beside hillside gully, near Kuminankira, ca. 1500 m., *L. S. Smith N. G. F.* 1098 (A, TYPE; LAE, BRI), October 1944, tree 36 m. overall, bole 24 m., narrowly buttressed, and channelled to 8 feet, diam. at breast height 2 feet, bark 9–18 mm. thick, outer shedding, in large, oblong flakes or strips of several of these united to form large irregular scales, after shedding surface very rough, inner bark red, with pale or green-tinged streaks on the back, sapwood



FIGURE 17. *Nothofagus grandis* Steen. a. twig, b. ♂ flowers on flush, c-g. cupules. (After L. S. Smith NGF 1098; a. nat. size, b-g. $\times 4$.)

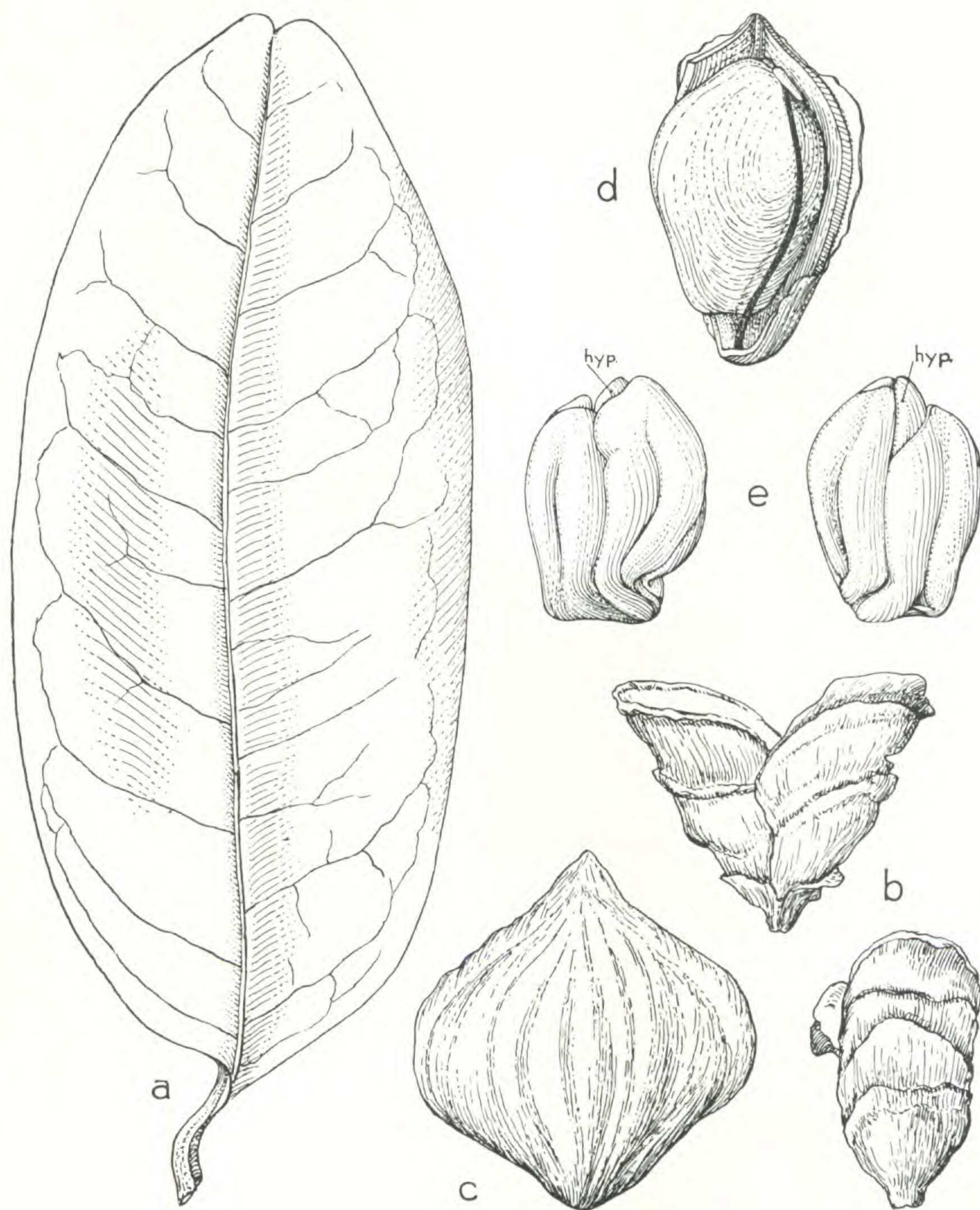


FIGURE 18. *Nothofagus grandis* Steen. a. leaf, b. two stipules, c. nut, d. one fruit shell with a seed on it, attached to the pseudo-raphe, at the top two aborted ovules visible, e. mature embryo from two sides, with folded cotyledons, hypocotyl directed apically. (After Womersley NGF 3389; a. nat. size, b-d. $\times 4$).

5–7.5 cm. thick, pale, heartwood brown (hard and said to be durable), flush pink to red, vern. *ufoiya* (Anona and Aiyura dialects), ripe fruit; Madang Distr., Aiyura, rain-forest, 1500 m., *A. J. Schindler s. n.* (LAE, BRI), September 1947, vern. *ifoiya*, young fruit; *ibid.* *A. J. Schindler s. n.* (LAE, BRI), July 1948, flowers appearing with flush in the end of July, flowering period appeared to last one week, ♂ and ♀ flowers and flush; Central Highlands, Aiyura, ca. 1800 m., *J. S. Womersley N. G. F. 3389* (LAE, L), November 26, 1950, tree 80 feet, bole 60 feet, girth 3 feet, not buttressed, fruits green, bark grey slightly scaly, underbark white, inner bark red-brown, becoming pale brown near the sapwood, sapwood white, heartwood brown, vern. *ifoya* (Aiyura dialect), *unuza* (Kamano dialect), fruiting; Mt. Hagen, *J. Cavanaugh N. G. F. 3320* (LAE, L), January-February 1950, sterile, probably from sapling, vern. *gripe*.

WEST NEW GUINEA: 6 km. SW of Bernhard Camp, 1140 m., *Brass & Versteegh 12553* (A), rare tree on ridge, in primary forest, tree 24 m. by 45 cm., crown not wide-spreading, bark brown, scaly, fissured, 7 mm. thick, sapwood light brown, heartwood dark red, sterile; *ibid.*, 4 km. SW of Bernhard Camp, Idenburg River, 900 m., *Brass & Versteegh 13147* (A, L), March 1939, common tree of mossy forest on ridge, 25 m. by 51 cm., bark 1 cm. thick, dark brown, scaly, sapwood rose, heartwood red, crown fairly wide-spreading, sterile.

The material is very satisfactorily homogeneous. The name has been chosen on account of the large nuts and large leaves.

Mr. J. S. Womersley, Forest Botanist, Lae, writes, March 17, 1953, that *N. grandis* produces such a desirable wood that they are hoping to develop a silvicultural technique for its propagation under plantation conditions. He kindly transmitted an extract from a report by Mr. E. Gray, Forest Officer, on observations near Aiyura, which is of interest to mention here.

Mr. Gray wrote: — "I encountered some very dense but scattered stands of *N. grandis* between Agunamura and Sophano where it attains a height of 45 m. and a D. B. H. of 105 cm. in many places. Even in the oldest and largest trees the heart is quite sound. Furthermore the bole is straight and cylindrical before it breaks into a large, rather untidy crown. A tendency to stag-headedness was noted in the over-mature trees.

"Unlike Territory rain forests in general, this species is found growing in practically pure stands in many instances. Regeneration of all ages is evident throughout these stands, in places quite dense. Unfortunately time did not permit of more than a cursory examination of the tree in its natural habitat, but I would say from what I saw that timber stand improvement work such as the felling of mature and over-mature stems would result in a very fine forest indeed.

"The stands are at present located mainly on the slopes and ridges in this country. The valley bottoms are grassland, undoubtedly high forest at one time, so it is impossible to say whether this species would naturally inhabit the lower reaches or not.

"The timber is favoured for building, bridge-decking and palings for gardens. It splits well and is durable in the ground for at least a number of years according to the local native inhabitants. I had another report of its durability from Mr. Fleil of the Lutheran Mission at Raipinka. He

told me that this same wood had been used as house stumps for sixteen years, removed and used a second time for the same purpose on a new building. The stumps showed little or no signs of decay when they were taken from the ground. Further, the wood is very attractive with a rich red heart and contrasting paler coloured sapwood. The tree seeds prolifically and there would be little difficulty in obtaining several pounds of seed annually."

13. *Nothofagus decipiens* Steen. in Blumea 7: 147. 1952. — FIG. 19.

Glabrous tree up to 25×1 m. Perules rounded, 1–1.75 mm. Leaves elliptic-oblong, coriaceous, $1.75\text{--}2.75 \times 1\text{--}1.5$ cm.; margins not very much recurved in the herb., both ends rounded, tip emarginate; midrib sulcate with an elevated ridge, very prominent on the undersurface; primary nerves

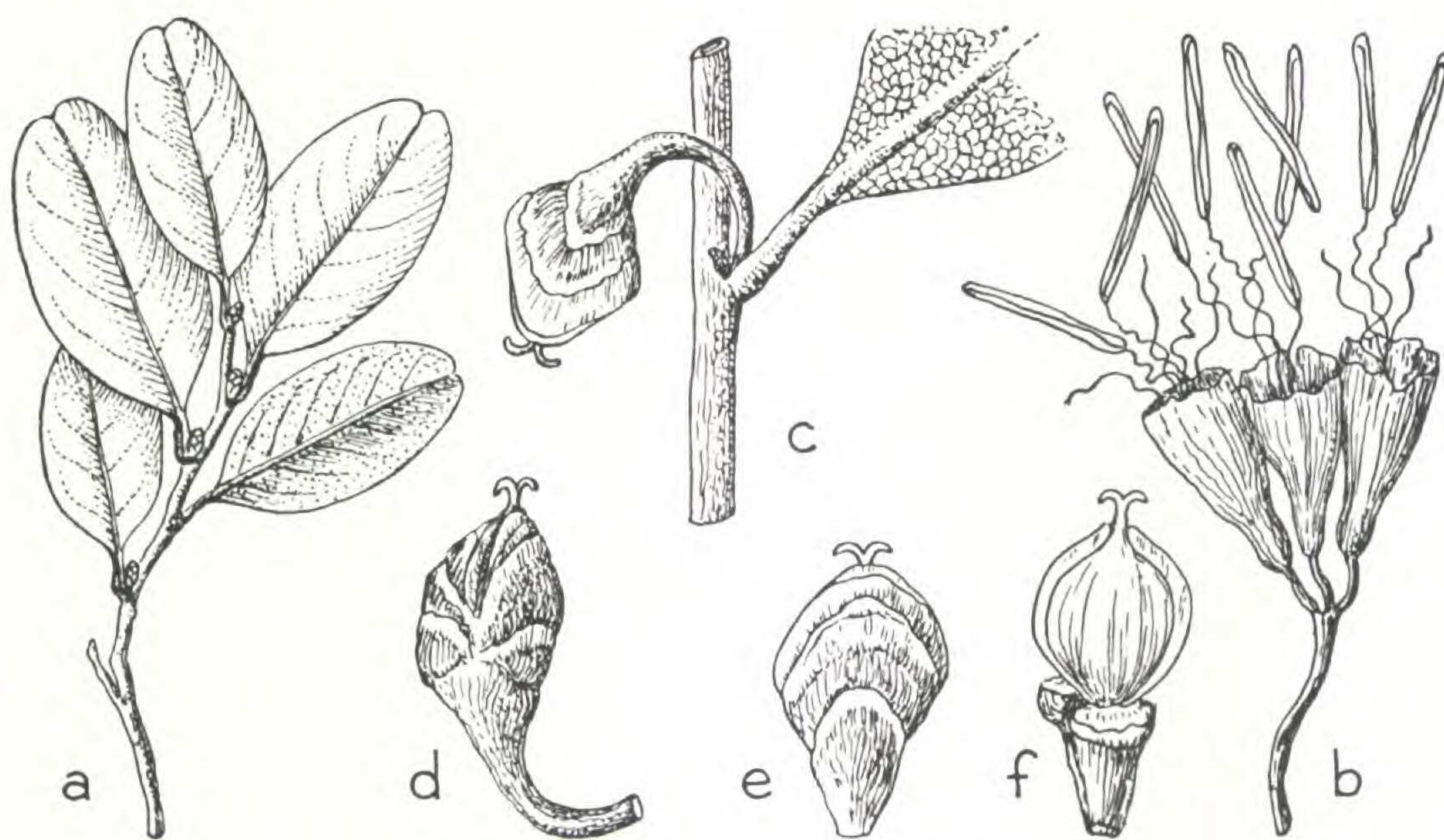


FIGURE 19. *Nothofagus decipiens* Steen. a. twig, b. triad of ♂ flowers, c–e. ♀ inflorescence, f. ♀ flower, cupule removed. (After Brass 12675; a. nat. size, b–f. $\times 4$.)

ca. 5 or 6 pairs, slightly prominent above, indistinct below. Reticulations fine-tessellate above, indistinct beneath; glands on undersurface 0.5–1 mm. spaced. Petiole 3–5 mm., semi-terete, margins elevated. Stipules early caducous, with a membranous margin, inserted distinctly below the middle, $6\text{--}7 \times 2.5$ mm. ♂ flowers (all detached), nearly sessile, or 1–1.5 mm. pedicelled, in 4–5 peduncled triads, erect, red, long-tubular, angular, perianth ca. 5 mm. long, with a constricted lower portion 1–1.25 mm. long. Stamens ca. 18; filaments sparsely hairy often mutually spirally twisted, longer than 2 cm., connate at the base; anthers linear, ca. 4 mm. long, connective glandular, tip apiculate. ♀ inflorescences on 6–7 mm. long recurved peduncles, peduncle slightly thickened towards the apex. Flowering cupule about as large as the ♀ flower, 2–3 lamellate. ♀ flower

glabrous, rounded, ca. 3 mm. through, wing broad, enclosing the base of the 0.5–0.75 mm. long style; stigmas broad. Ripe cupule and nut unknown.

WEST NEW GUINEA: Central part: 18 km. SW of Bernhard Camp, Idenburg River, 2150 m., *L. J. Brass 12675* (L, TYPE; A, BO), February 1939, dominant tree in mossy forest, co-dominant with *N. bernhardi* in these forests, on slopes of ridges, up to 25 m. tall, 1 m. diam., branches thinly foliated and somewhat flat-spreading, leaves reddish when young, ♂ and ♀ flowers and young fruit, male flowers red.

I found no male flowers attached to the twigs, all were loose as if they had dropped from above and had been caught by the leaf axils or the resinous sticky parts of the foliage. It could be, of course, that these wind-dispersed male flowers belong to another species growing in the same forest. I do not assume the tree to be dioecious.

Habitually this species closely resembles 7. *N. cornuta* but differs in the long-peduncled, recurved, 2–3-lamellate cupules and roundish female flowers. It also resembles 1. *N. recurva* but possesses only one female flower per cupule and long-peduncled male flowers (if they belong to it). Thirdly it resembles 15. *N. eymae* but differs in the long-peduncled, early and distinctly recurved cupules.

14. *Nothofagus rubra* Steen. in *Blumea* 7: 147. 1952. — FIG. 20.

Glabrous tree, up to 23 m. and 64 cm. diam.; twigs rather stout. Perules coarse, distinctly imbricate, $5-6 \times 2.5$ mm., quadrangular, long-persistent about the base of the twigs. Leaves ovate-oblong, hard-coriaceous, margin entire, $\pm$ recurved, $2.5-4.5 \times 1.5-3$ cm., apex and base both rounded, upper surface smooth not reticulate, undersurface with fine-netted but not prominent reticulations; nerves ca. 6 pairs; glands (0.5–) 0.75–1 mm. apart. Petiole 4–5 mm. Stipules oblong, rather early caducous, $5-8 \times 2.5-3$ mm. ♂ flowers in erect, sessile or subsessile triads on efoliate short-shoots or on twig ends with leaves. Perianth tubular, later slightly widened, 5–6 mm. long, the central flower of the triad sometimes pedicelled, with a short cupular limb 3 mm. long. Stamens 10–12; filaments at least 2 cm. long, sparsely pubescent towards the apex; anthers 4 mm. ♀ inflorescences very few, erect, sessile. Flowering cupule narrower and shorter than the ovary, very convex, with free, unequal valves, one entire, the other sometimes irregularly lobed, $5.5-6 \times 2.5-3$ mm.; lamellae 2. ♀ flower solitary, orbicular, rather thick, hardly winged, perianth-shoulder ending far below the style-base, 6–7 mm. diam.; style thick, 2 mm.; stigmas 0.5 mm. Nut (?mature) orbicular, 4 mm. diam.; style 1.5 mm., persistent.

WEST CENTRAL NEW GUINEA: 18 km. SW of Bernhard Camp, Idenburg River, 2200 m., *Brass & Versteegh 11997* (A, TYPE; L), February 1939, abundant tree in primary forest on slopes of ridges, tree 23 m., 64 cm. diam., crown not wide-spreading, fruit brown-green, bark 12 mm. thick, dark brown, fissured, scaly, rough, sapwood brown, heartwood brown; *ibid.*, *Brass & Versteegh 11997a*, February 1939, tree abundant in primary forested ridges, flowering material of no. 11997, ♂ flowers rose, female reddish green. Wissel Lake region:

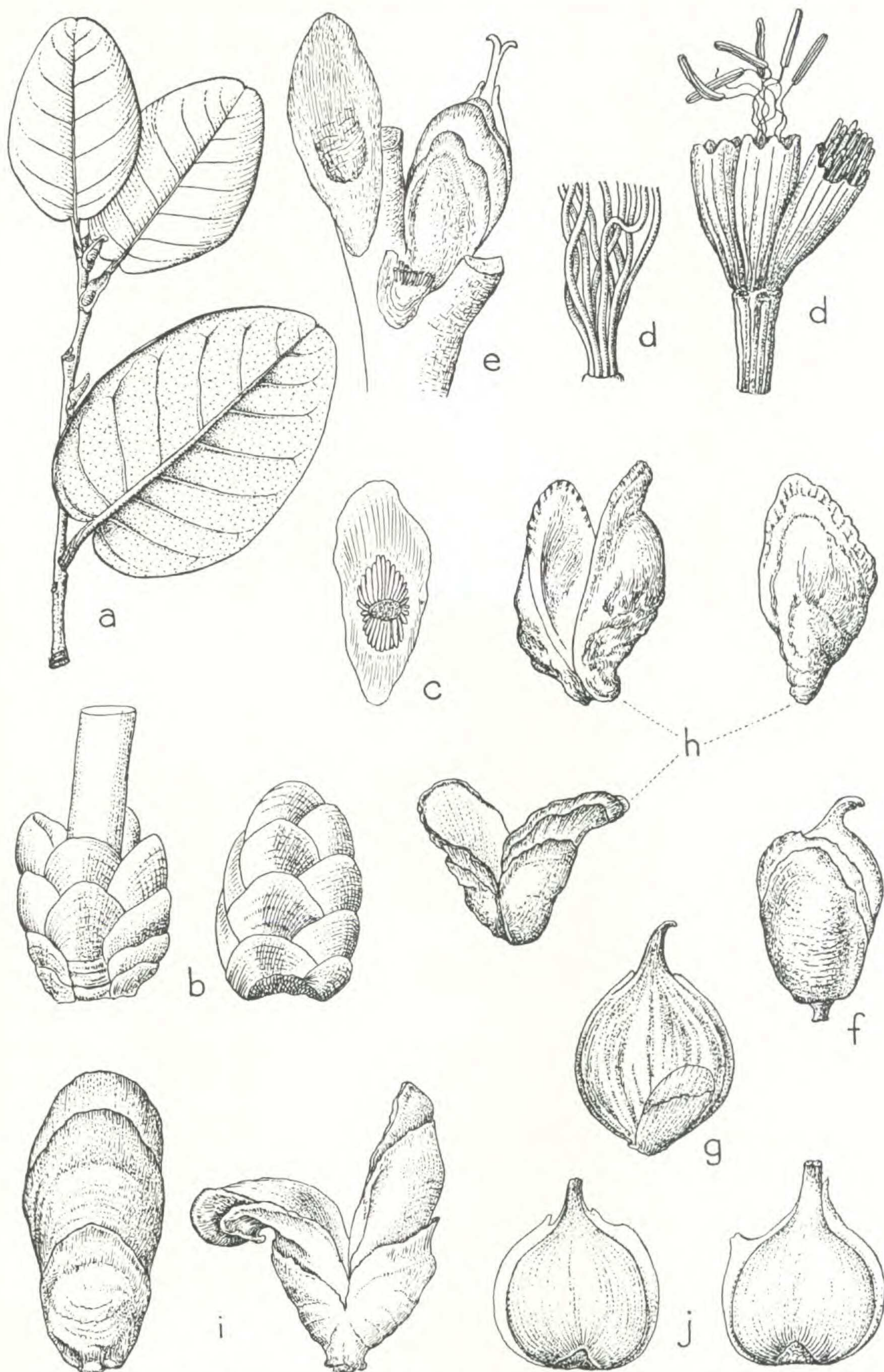


FIGURE 20. *Nothofagus rubra* Steen. a. twig, b. perular bracts, c. stipule, inner side, d. triad of ♂ flowers, d'. insertion of stamens in bud, e. flowering cupule with part of removed stipule below it, f. half-mature cupules, g. same, from other side, h. three older cupules, i. two ?ripe cupules, j. ?ripe nuts. (After Brass & Versteegh 11997; a. nat. size, b. $\times 5$, c-j. $\times 4$.)

Bivouac Digatara Pass, *Eyma* 5387 (L, BO), October 1939, sterile; *ibid.*, Bubeiro, 1750–1810 m., *Eyma* 4870 (BO, L, A, K, SING, BM, P, CAL, BISH), April 13, 1939, sterile.

15. *Nothofagus eymae* Steen. in *Blumea* 7: 147. 1953. — FIG. 3, 21.

Monoecious glabrous ?tree. Twigs subterete. Perules roundish, 1.5 mm. Leaves about elliptic, rounded at both ends, coriaceous, shining above, $2-3.25 \times 1.25-1.75$ cm., margin rather distinctly recurved, apex distinctly emarginate; midrib sulcate with elevated ridge; side-nerves ca. 5 pairs, slightly prominent on both sides; reticulations indistinct on both surfaces; glands rather wide apart on the lower surface, 0.75–1.5 mm. spaced.

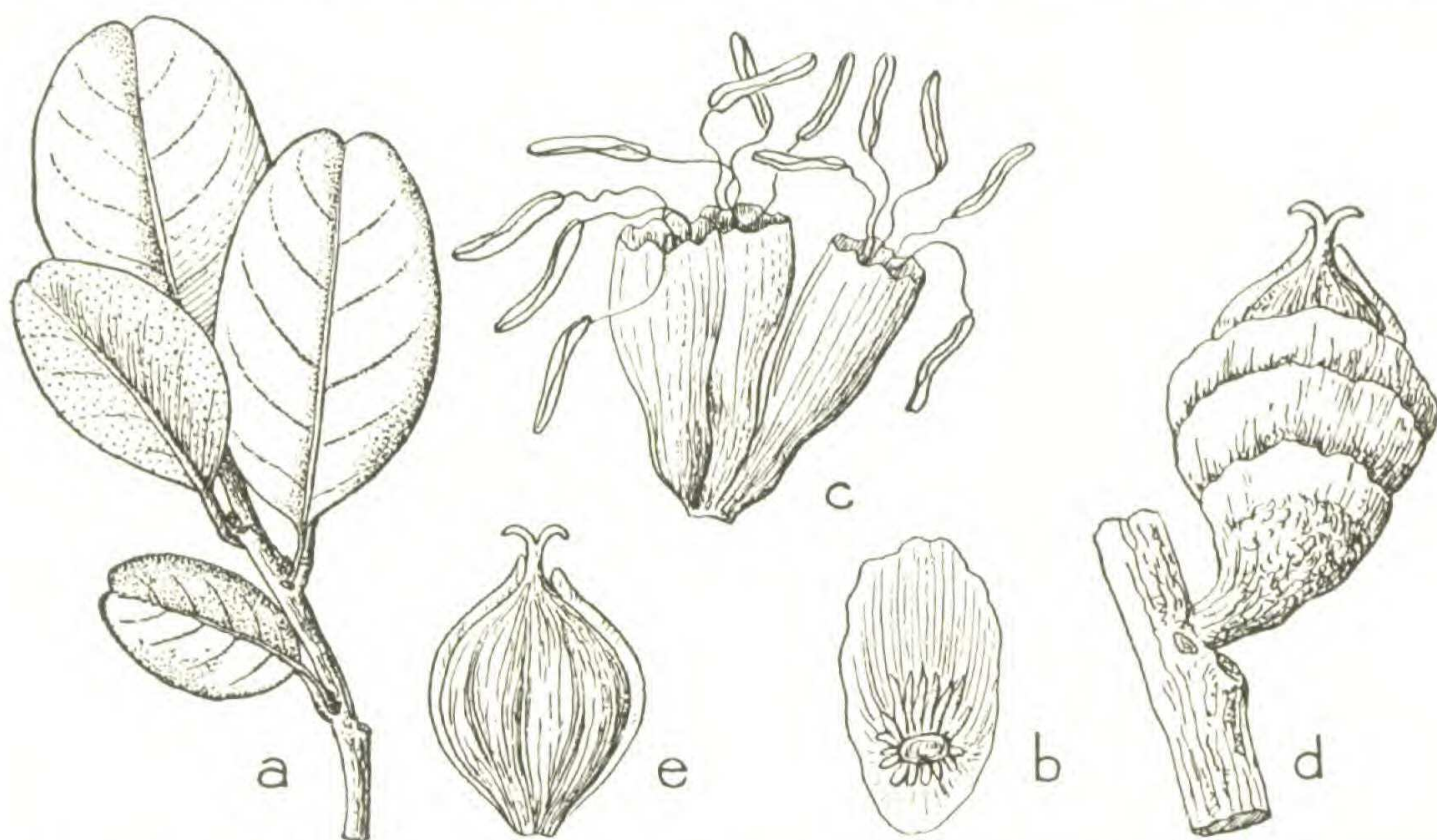


FIGURE 21. *Nothofagus eymae* Steen. a. twig, b. stipule, inner side, c. triad of ♂ flowers, d. flowering cupule, e. ♀ flower. (After *Eyma* 4800; a. nat. size, b–e. $\times 4$.)

Petiole 2–5 mm. Stipules only on the flush, oblong, $4-5 \times 2-3$ mm., attached in the lower part. ♂ flowers in subsessile triads, sessile, narrow tubular, ca. 4–5 mm. long, limb truncate. Stamens ca. 12, filaments slightly puberulous, anthers small, 2–2.5 mm. long, tip apiculate. ♀ cupule $\pm$ sessile, $\pm$ oblong, 5–6 mm. long, valves with 2 distinct lamellae. ♀ flower roundish, 4×3.5 mm., winged towards the apex; style enveloped by the perianth limb, very short; stigmas 0.5 mm. Ripe cupule possibly erect, not known. Nut unknown.

WEST CENTRAL NEW GUINEA: Wissel Lake region, observed between Enarotali to Kugapa and Egogitoagapa to Enarotali, *Eyma* 4800 (BO, TYPE; L), March 29, 1939; 15 km. SW of Bernhard Camp, Idenburg River, 1760 m., *Brass & Versteegh* 11963 (A, L), January 1939, abundant tree of primary forest on slope of ridge, mossy forest, co-dominant with *Weinmannia urdanetensis* Elmer, tree 26 m. $\times$ 43 cm., crown not wide-spreading, bark 8 mm. thick, gray, scaly, wood brown, sterile.

This species resembles 1a. *N. recurva* var. *microphylla*, but the cupule is one-flowered, $\pm$ sessile and not recurved. It also resembles 5. *N. pullei* but is glabrous. It shows most resemblance to 11. *N. bernhardi*, but the

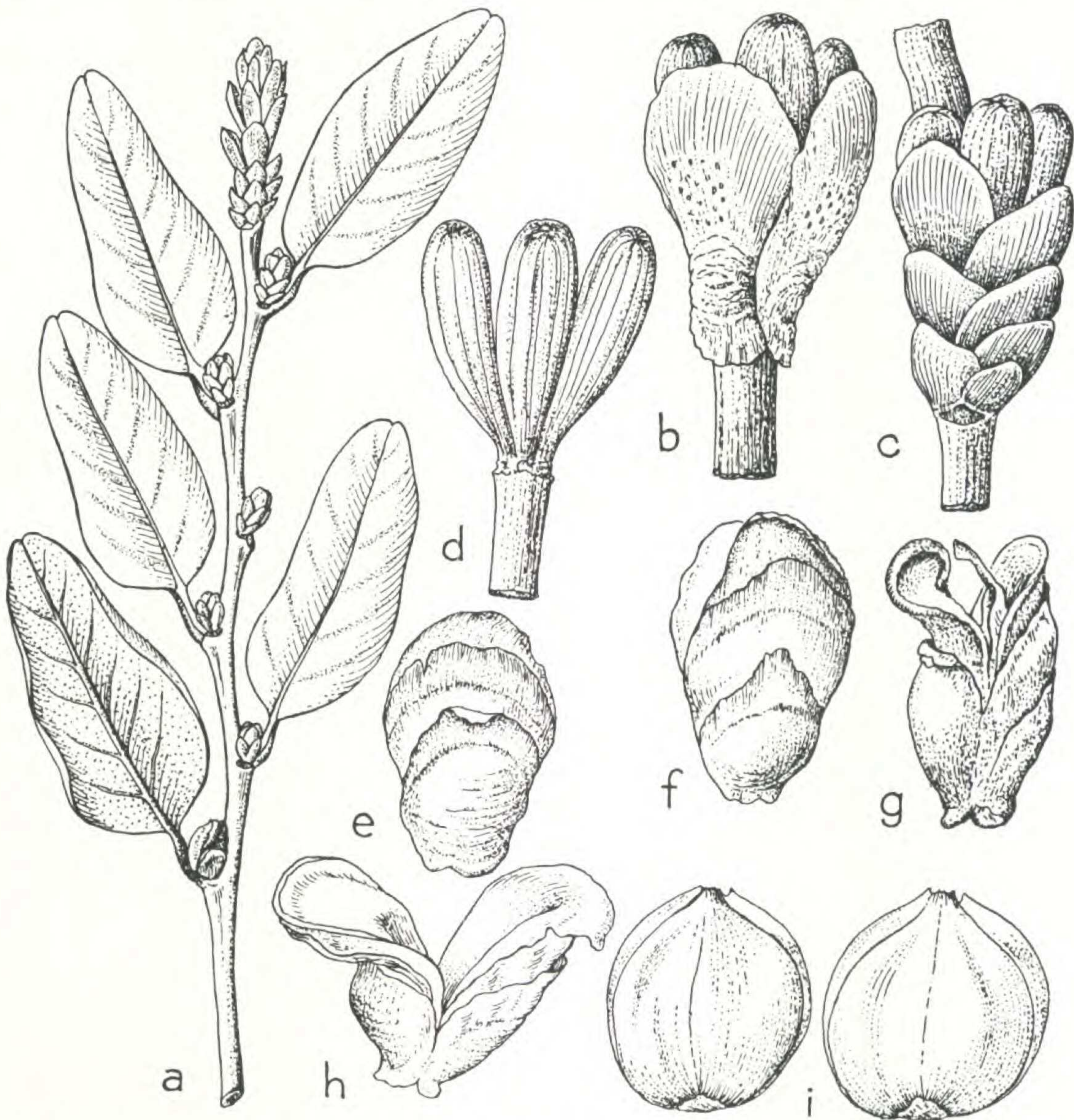


FIGURE 22. *Nothofagus dura* Steen. a. twig, b. triad of δ flowers on base of flush enclosed by 2 stipules, c. ditto, in axil of higher perular bracts, d. triad of δ flowers, e-h. cupules, i. two nuts. (After Brass & Versteegh 10443; a. nat. size, b-i. $\times 4$.)

cupule is different in the early stage, and later the female flowers are not ovate-oblong.

16. *Nothofagus dura* Steen. in *Blumea* 7: 147. 1952. — FIG. 22.

Monoecious tree up to 33 m. high, 0.5 m. diam. Twigs brownish, rather stout. Perules roundish, 2 mm. diam. Leaves hard-coriaceous, ovate-oblong, base cuneate to rounded, margin entire, recurved, $2.75-4.5 \times 1.25-1.75$ cm.; nerves ca. 7 pairs, distinct on the lower surface, hardly

visible on the upper surface; reticulations not visible above, dense, slightly prominent below; glands 0.5–1 mm. apart. Petiole 4–5 mm. Stipules not very early caducous, 8–9 × 4 mm. ♂ flowers in triads, sessile, at the base of the flush, partly in perular axils; perianth 6 mm. Stamens 12; anthers 4–5 mm. ♀ inflorescences probably sessile, 1-flowered. ♀ flower unknown (in one aborted flower the style 1.5 mm.). Mature cupule sessile, split at least halfway, oblong, ca. 8–10 × 4–5 mm., hard, woody; lamellae 2. Nut suborbicular, 5–6 mm. diam., the basal part thickened.

WEST CENTRAL NEW GUINEA: 9 km. NE of Lake Habbema, 2840 m., *Brass & Versteegh 10443* (L, TYPE; A, BO), Oct. 1938, dominant in mossy forest, tree 38 m. × 47 cm., crown not wide-spreading, ♂ flowers rose, fruit brown, bark rough, gray-brown, 8 mm. thick, fissured, scaly, outer wood white, inner red-brown.

This species resembles 1. *N. recurva* in habit but is very different in the sessile (not recurved), 1-flowered cupule. It differs from 4. *N. brassi* in the sessile, much smaller, 1-flowered cupule, and from 15. *N. eymae* in the leaf shape.

SPECIES DUBIA

Nothofagus sp.

EAST NEW GUINEA: Mt. Hagen, *J. Cavanaugh N. G. F. 3323* (LAE), January–February 1950, vern. *gripe*.

This sterile specimen resembles 3. *N. starkenborghi* in leaf shape, but the leaf differs in the distinct prominent ridge on the sulcate midrib. The material is too imperfect for identification.

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FLORA MALESIANA FOUNDATION,
LEYDEN, THE NETHERLANDS.

INDEX TO FAGACEOUS NAMES

- Betula antarctica* Willd., 338
Calucechinus Hombr. & Jacq., 332, 334
 antarctica (Forst.) Hombr. & Jacq., 335
 montagni Hombr. & Jacq., 335
Calusparassus Hombr. & Jacq., 333, 336
 betuloides (Mirb.) Hombr. & Jacq., 338
 forsteri (Hook.) Hombr. & Jacq., 338
 pumilio (Poepp. & Endl.) Hombr. & Jacq., 336
Castanea sativa Mill., 334
Fagaster Spach, 332
Fagus, 326
 alpina Poepp. & Endl., 335
 antarctica Forst., 335
 betuloides Mirb., 338
 carroni C. Moore, 337
 cliffortioides Hook. f., 338
 cunninghami Hook. f., 337
 dombeyi Mirb., 338
 dubia Mirb., 338
 forsteri Hook., 338
 fusca Hook. f., 337
 var. *colensoi* Hook. f., 337
 glauca Phil., 334
 gunnii Hook. f., 335
 menziesii Hook. f., 337
 moorei F. v. M., 337
 nervosa Phil., 334
 nitida Phil., 338
 obliqua Mirb., 335
 procera Poepp. & Endl., 335
 procera Salisb. *nom. nud.*, 335
 pumilio Poepp. & Endl., 336
 sect. *Eufagus* A. DC., 333
 sect. *Nothofagus* A. DC. em. B. & H., 333
 solandri Hook. f., 338
 subgen. *Calucechinus* (Hombr. & Jacq.) Miq., 333
 subgen. *Calusparassus* (Hombr. & Jacq.) Miq., 333
 truncata Colenso, 337
 uliginosa Phil., 335
 valdiviana Phil., 335
Lophozonia Turcz., 333, 334
 heterocarpa Turcz., 335
Nothofagus, 326, 332
 alessandri Espinosa, 335
 alpina (Poepp. & Endl.) Oerst., 335
 antarctica (Forst.) Oerst., 335
 apiculata (Colenso) Krasser, 337
 bernhardi Steen., 361
 betuloides (Mirb.) Oerst., 338
 blairii (Kirk) Krasser, 337
 brassi Steen., 350
 carri Steen., 359
 cliffortioides (Hook. f.) Oerst., 338
 Nothofagus cornuta Steen., 359
 crenata Steen., 355
 cunninghami (Hook. f.) Oerst., 337
 decipiens Steen., 367
 dombeyi (Mirb.) Oerst., 338
 dura Steen., 371
 eymae Steen., 370
 fusca (Hook. f.) Oerst., 337
 x *cliffortioides*, 315
 x *solandri*, 315
 glauca (Phil.) Krasser, 335
 grandis Steen., 363
 gunnii (Hook. f.) Oerst., 335
 leoni Espinosa, 336
 megalocarpa Reiche, 334
 menziesii (Hook. f.) Oerst., 337
 montagn(e)i (Hombr. & Jacq.) Reiche, 335
 moorei (F. v. M.) Krasser, 337
 nervosa (Phil.) Dimitri & Melano, 334
 nitida (Phil.) Krasser, 338
 obliqua (Mirb.) Oerst., 335
 var. *macrocarpa* DC., 335
 patagonica Gandoger, 338
 perryi Steen., 347
 procera (Poepp. & Endl.) Oerst., 335
 pseudoresinosa Steen., 358
 pullei Steen., 353
 pumilio (Poepp. & Endl.) Krasser, 336
 recurva Steen., 343
 var. *microphylla* Steen., 345
 resinosa Steen., 356
 rubra Steen., 368
 sect. *Calucechinus* (Hombr. & Jacq.) Krasser, 334
 sect. *Calusparassus* (Hombr. & Jacq.) Krasser, 336
 sect. *Deciduae* Steen., 334
 sect. *Planae* Steen., 336
 sect. *Plicatae* Steen., 334
 sect. *Sempervirentes* Steen., 336
 series *Triflorae* Steen., 338
 series *Uniflorae* Steen., 338
 solandri (Hook. f.) Oerst., 338
 starkenborghi Steen., 347
 subgen. *Lophozonia* Krasser, 333, 334
 subgen. *Molischia* Krasser, 333
 subsect. *Antarcticae* Steen., 334
 subsect. *Bipartitae* Steen., 338
 subsect. *Pumiliae* Steen., 336
 subsect. *Quadripartitae* Steen., 337
 subsect. *Tripartitae* Steen., 338
 truncata (Colenso) Cockayne, 337
 x *solandri*, 315
Parafagus Oliver, 333
 otakonia Oliver, 330